NATURAL FOOD AND PREDATORY ACTIVITY OF THE PADDLE CRAB, *Ovalipes catharus*: A FLEXIBLE FORAGER

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" AT PRESENT, IT IS NOT UNREASONABLE TO CLAIM
THAT PADDLE CRABS ARE MORE SOPHISTICATED
THAN MODELS ... (AND MODELERS) "

S.Dog., 1986.

PRELUDE

This Thesis is divided into two chapters, the first chapter contains experiments undertaken in the laboratory on the feeding behaviour of the paddle crab *Ovalipes catharus*. These experiments are divided into two parts. Part 1 deals with prey selection and foraging behaviours of paddle crabs, and part 2 deals with improvement of predator efficiency by *O. catharus*. Chapter 2 includes all field studies on the natural food and availability of paddle crab prey.

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MUSSEL SELECTION BY THE PADDLE CRAB

Key Words: PORTUNIDAE, *OVALIPES*, OPTIMAL FORAGING, PREDATOR-PREY, HANDLING TIME, REJECTION TIME.

INTRODUCTION

It is well known that crabs feed on bivalve molluscs and studies have shown that predators can influence these populations (Ebling et.al., 1964; Virstein, 1977; Hill, 1979; Blundon and Kennedy, 1982b; Boulding, 1984; Boulding and Hay, 1984; Du Preez, 1984). Recent studies have investigated the factors affecting prey selection in crabs (Hughes, 1979; Hughes and Elner, 1979; Elner, 1980; Hughes and Seed, 1981; Cunningham and Hughes, 1984) and these studies, based on the energy maximization premise, suggest that the predator chooses its diet to maximize the net energy intake per unit foraging time (Charnov, 1976; Emlen, 1968; Pulliam, 1974; Elner and Hughes, 1978; Hughes, 1980). For limited visual predators such as crabs Elner and Hughes (1978) and Hughes (1979) have incorporated finite prey recognition times, prey misidentification and the effect of learning into their model.

Previous studies on crabs suggest energy intake from particular sized prey changes with crab size and species (Elner and Hughes, 1978; Hughes and Seed, 1981; Jubb et.al., 1983). However, to date no consistent pattern has been determined for portunid crabs. The aim of this study is to explain the behavioural patterns of prey selection by the paddle crab, O. catharus including the criteria for acceptance or rejection of particular prey sizes and the influence of density on prey size selection. During all experiments handling times were measured and used for calculation of profitabilities.

The paddle crab, Ovalipes catharus (Brachyura:Portunidae) occurs abundantly in shallow subtidal habitats off most sandy beaches throughout New Zealand (Wear, 1984). They are regarded as opportunists, feeding on a wide variety of items including plant material, benthic invertebrates, fish and bivalves

(Kung, 1973). Field information suggests that these crabs may concentrate on certain prey types if locally abundant (Chapter II) and Wear (1984) suggested swimming crab predation may be an important factor contibuting to the decline of shellfish stocks in coastal waters. While mussels may only form part of the natural diet of O. catharus , the behavioural responses recorded here are likely to operate on many bivalve species which have a patchy distribution within the sandy shore benthos.

MATERIALS AND METHODS

Paddle crabs were collected from South Brighton beach, Canterbury, New Zealand, using an Otter trawl towed within a distance of 1 km from the surf zone during February and March 1984 and 1985. Only male crabs were used in experiments to avoid potential bias caused by sexual differences in morphology and predation behaviour. The carapace width of each crab was measured and the cross sectional dimension of the major chela recorded, crabs with abnormal chelipeds were rejected. Crabs were kept individually in plastic aquaria (60cm x 35cm) filled to a depth of 10cm with closed circuit running seawater at 18°C. To standardize hunger levels newly caught crabs were starved for 3 days prior to use.

The blue mussel, Mytilus edulis aoteanus was used in all feeding experiments in order to minimize pre-capture experience, it being absent from the natural diet of the paddle crab (Chapter II). Mussels were collected from the upper mid-tidal zone of an exposed shore situation, thereby standardizing shell characteristics which may vary with exposure and tidal level (Seed, 1980). They were sorted and measured to the nearest 0.1cm and any fouling organisms removed. In order to ensure mussel consistency and freshness, collections were made weekly and only undamaged mussels in good condition were used as prey.

All experiments used two size categories of crab, small 50-60mm and large 80-90mm carapace width. Handling times were determined for 4 crabs of each size group fed on individual mussels ranging from 0.5cm to 3.5cm length. A total of 22 and 25 prey were fed to small and large crabs respectively. The size of mussels used were selected randomly and a maximum of 5 prey were presented to each crab. Each mussel was gently lowered into the tank and

the following events timed.

a) Opening time. Defined as the time from the crab's first physical contact with the prey item, through the period of prey manipulation to shell entry and the first bite of exposed flesh taken.

b) Eating time. Defined as the period beginning at the first bite through further prey manipulation to the point where the meal was completed and the last part of the shell rejected.

c) Handling time. Defined as the summation of opening and eating time.

Individual handling times were used in the determination of prey profitability defined by Hughes and Seed (1981) as dry flesh weight of mussel (mg) / handling time (min). Mussel dry weights were calculated according to the regression equation:

$$\ln \text{Weight(g)} = 2.78 \ln \text{length(mm)} - 10.99$$

$r = .99$, $n = 20$ (Davidson, 1984).

Equal ratio experiments were designed to determine predator prey selection using 7 small and 11 large crabs. Each crab was individually presented with 6 size categories of mussel, each represented by 12 individuals ranging from 0.5 to 3.5cm in 0.5cm length groups. The 72 mussels were scattered randomly on the aquarium floor. The number of mussels eaten daily was monitored for 12 days with eaten mussels being replaced by prey of similar size.

To investigate the influence of prey size and encounter rates paired ratio experiments used 3 size classes of mussels, small (0.5-1.0cm), medium (1.5-2.0cm) and large (2.5-3.0cm) length. In the first series of paired ratio experiments, large crabs (80-90mm cw) were presented with combinations of small:medium mussels as follows-5:5, 10:5 and 20:5. Further experiments

were done using the same combinations of large and medium mussels. All 3 size groups of mussels could be consumed using the same opening techniques. Each crab was observed continuously for approximately 1.5 hours noting acceptance-rejection sequences and handling times. Only mussels which were actively handled and presumably recognised as prey were recorded as encounters. Those touched but not handled were excluded from calculations as they were clearly not recognised as prey. All mussels consumed were replaced by ones of similar size in order to maintain prey proportions.

RESULTS

Mussel Opening Techniques

Following the introduction of prey to the aquaria, O. catharus would usually become active moving about the aquaria floor extending the chelipeds in a sweeping motion and moving the walking legs in a digging action. This suggests that swimming crabs are able to detect prey at a distance through the water probably by chemoreceptors on the antennules. Visual response was restricted to movement, no visual detection of mussels was observed. Contact with prey either with the walking legs or chelae resulted in acceleration of activity leading to the mussel being drawn towards the mouth. Here it was manipulated not only by the dimorphic chelae (Fig.1) but also by the first 2 pairs of walking legs and the 3rd pair of maxillipeds. Periods of prey opening activity were often interrupted by periods of inactivity, this usually increased in duration with prey size. Such inactivity may indicate rest periods between bouts of prolonged opening activity.

Crabs attacked the prey using five distinct opening techniques.

1) Direct Crushing. Small mussels (< 1.0cm length) were crushed outright. The prey was held by the left (cutter) chela, while the larger (crusher) chela crushed the prey. Very small mussels were passed to the maxillipeds where they would be manipulated to a position where the mandibles could crush the shell.

2) Anterior Crushing. Mussels between 1.0 and 3.5cm length, were held at the anterior end by the mouth parts while the cutter chela held the posterior part of the shell over the adductor muscle (Fig.2). The crusher chela was then applied to the anterior or unbonal end of the mussel. The prey was frequently turned or slightly adjusted by the cutter chela

following unsuccessful crushing attempts. Examination of opened mussels from the feeding experiments indicated that this technique was most frequently used for mussels between 1.0cm and 3.0 cm. Elner (1978) reported this technique to be the most common and most successful used by another portunid crab, Carcinus maenas on the mussel M. edulis .

3) Posterior Crushing. This technique was often used alternately with anterior crushing. Mussels between 1.0 and 3.5cm were rotated 180 degrees from the anterior crushing method bringing the posterior end to the mouthparts. The cutter chela held the umbone while the crusher chela squeezed the posterior end of the mussel over the adductor muscle. This technique, although taking longer than anterior crushing to open prey, inflicted greater damage to the shell.

4) Wedging. This relatively slow method was used when attacking mussels which proved too robust or too large to crush. The crusher chela was used to wedge a passage between the valves. This allowed either cutting of the adductor muscle by the cutter chela leaving the prey defenceless or would weaken the shell sufficiently to make a previously unsuccessful method successful (Fig.3).

5) Edge-chipping. This technique was also used when prey failed to yield or was used on large or thick shelled individuals. Both chelipeds grasped the prey with the posterior edge of the mussel aligned to the mandibles. As the mandibles crushed the posterior edge of the shell the chelipeds pulled the prey away from the mouth. This mandible action resulted in removal of chips along the posterior edge weakening the shell sufficiently to make one of the other techniques successful or allow access of a cheliped.

When attacking a mussel, O. catharus often used a series of opening techniques, these appeared to be a function of mussel size. The 5 methods adopted, however, remained relatively consistent on all occasions and for all crabs.

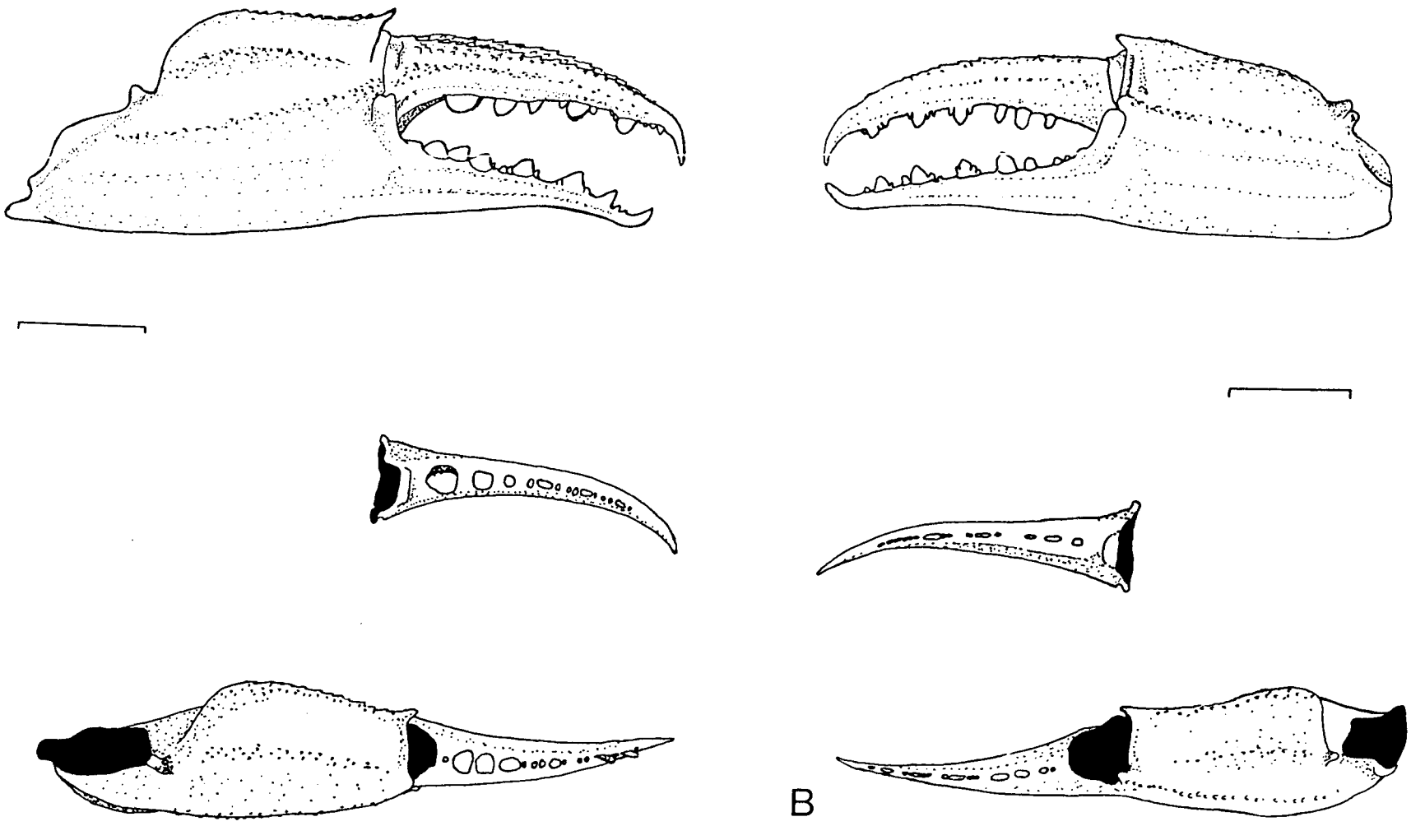


Fig. 1. Crusher (a) and cutter (b) chela of a male paddle crab Ovalipes catharus, carapace width 75 mm, with occlusive surfaces of dactyli (above) and propi (below); scale bar = 10 mm. (a) ln crusher height = 0.94 ln carapace width -0.55; (b) ln cutter height = 0.95 ln carapace width -0.58.

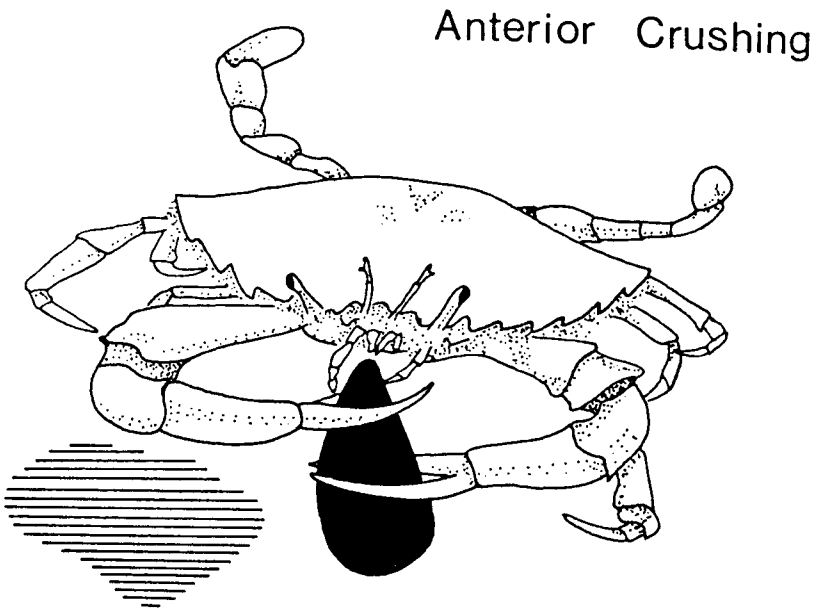


Fig.2. Anterior crushing technique adopted by Ovalipes catharus feeding on Mytilus edulis aoteanus

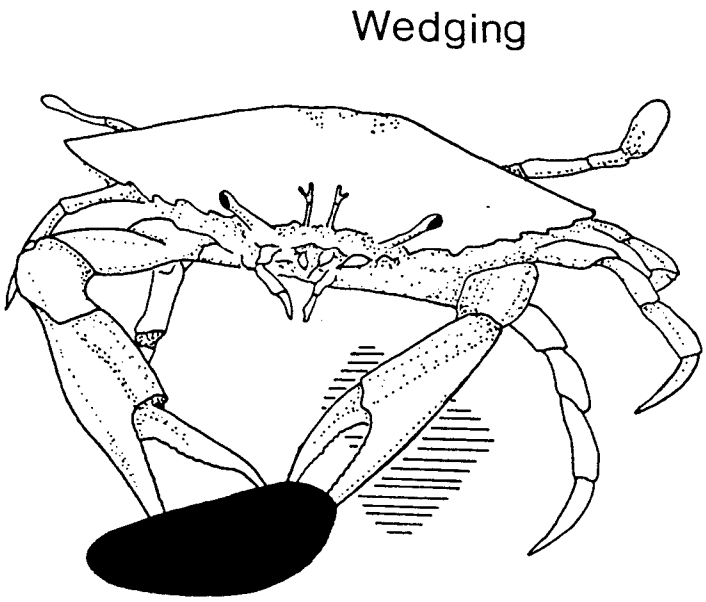


Fig.3. Wedging technique adopted by Ovalipes catharus feeding on Mytilus edulis aoteanus .

Handling Times

When plotted against prey size opening and eating time varied between crabs (Fig.4). Handling time variation occurred as crabs employed different opening techniques depending upon prey size, strength and probably vulnerability.

Opening times increased dramatically with prey length (Fig.4). As direct crushing failed, crabs adopted the slower anterior or posterior crushing techniques. The prey size at which this change occurred increased with crab size. For small crabs between 1.0 and 1.3cm prey length and for large crabs between 2.2 and 2.5 cm prey length.

Eating time curves reflected the ability of the larger crabs to eat a greater volume of flesh in a shorter period of time. However, the rate at which large and small crabs handled very small mussels (<1.2cm) was similar. Large crabs attacking very small mussels therefore gained no advantage through strength, however, the similar handling times to small crabs suggested increased chela size was no disadvantage.

The regression line relating opening time and mussel length followed an exponential function (logarithmic transformation of dependent variable) while power functions (log transformations of both variables) best described the relationship for eating and handling times against prey length (Figs.4b,5). Analysis of covariance (log transformed data) for opening, eating and handling times for small and large crabs all revealed significantly different slopes and intercepts ($P<.001$). Slopes of regression lines for small crabs were steeper than those recorded for large crabs. This suggested that chela size and probably strength significantly altered handling operation rates between the two size categories of crab.

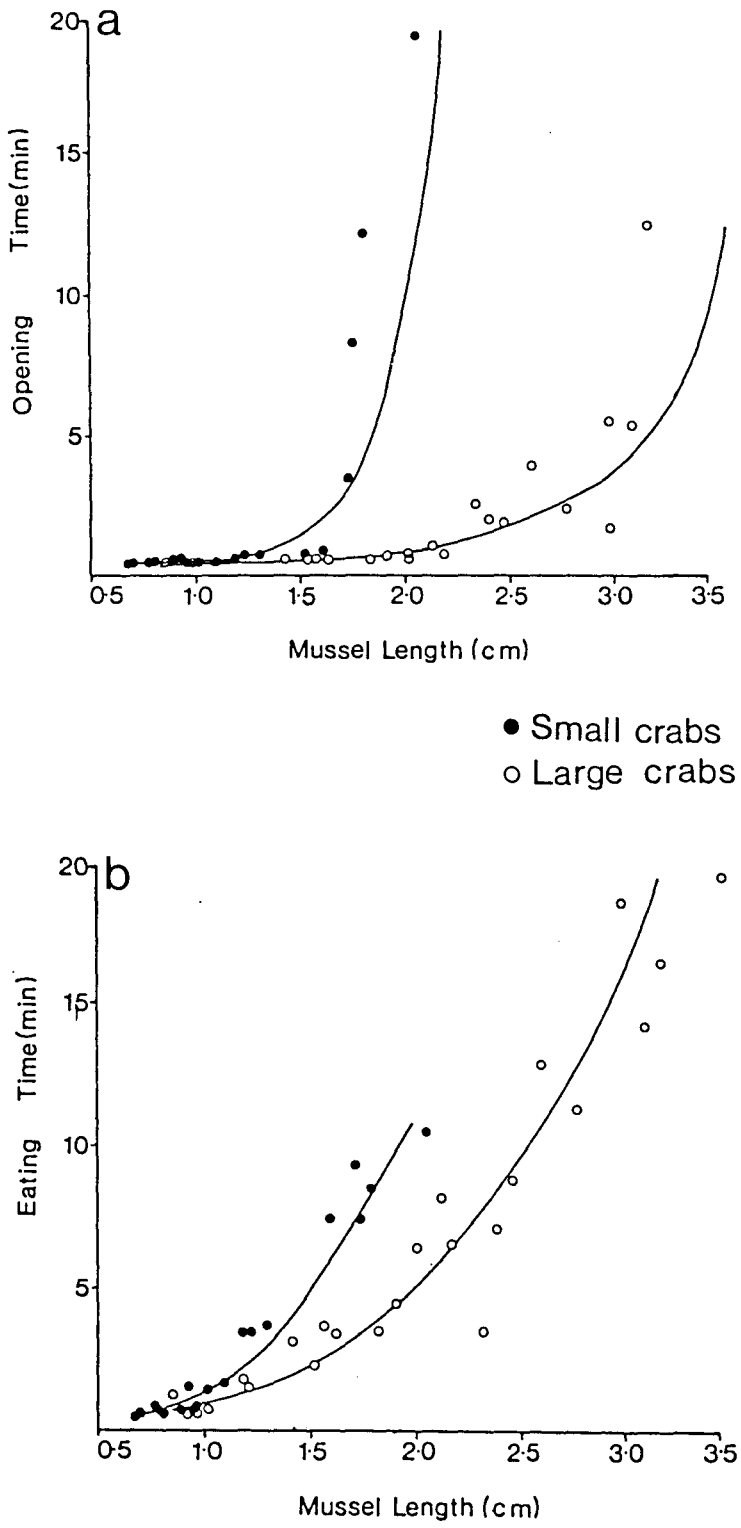


Fig.4. Prey size versus time taken by two size categories of O. catharus to (a) open and (b) eat individual M. edulis aoteanas: (a) • Crabs 50–55mm, $\ln Y = -5.70+0.391X$, n=32; o Crabs 80–85mm, $\ln Y = -4.27+0.181X$, n=25 (b) • Crabs 50–55mm, $Y = .000097X^{3.96}$, n=22; o Crabs 80–85mm, $Y = .00052X^{3.04}$ n=25

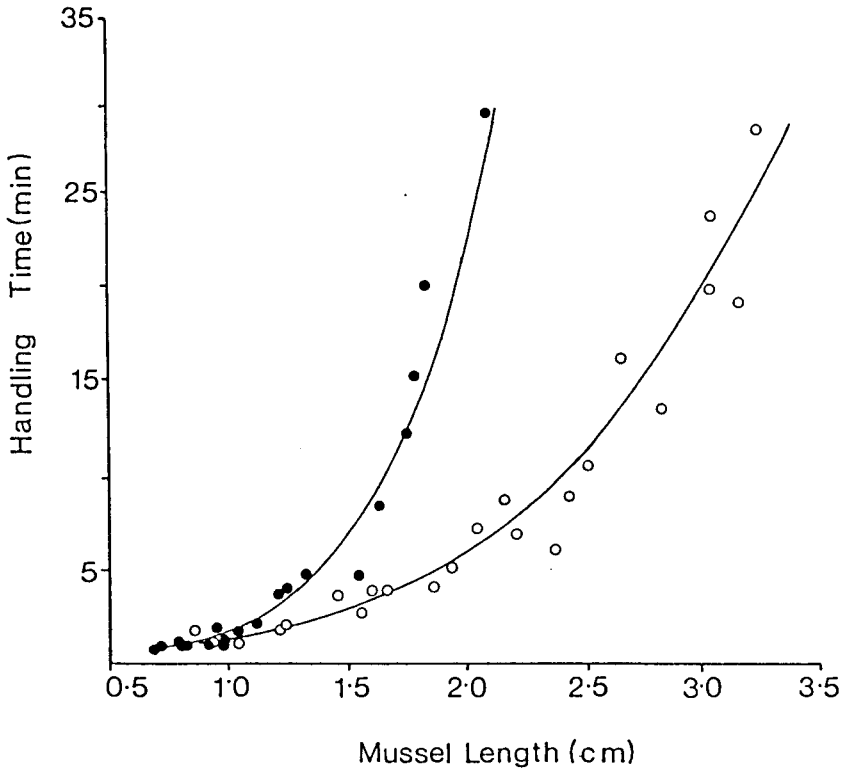


Fig.5. Prey size versus time taken by two size categories of O. catharus to handle individual mussels: • Crabs 50–55mm $Y = .00006X^{4.29}$, n=22; c Crabs 80–85mm $Y = .00053X^{3.09}$, n=25

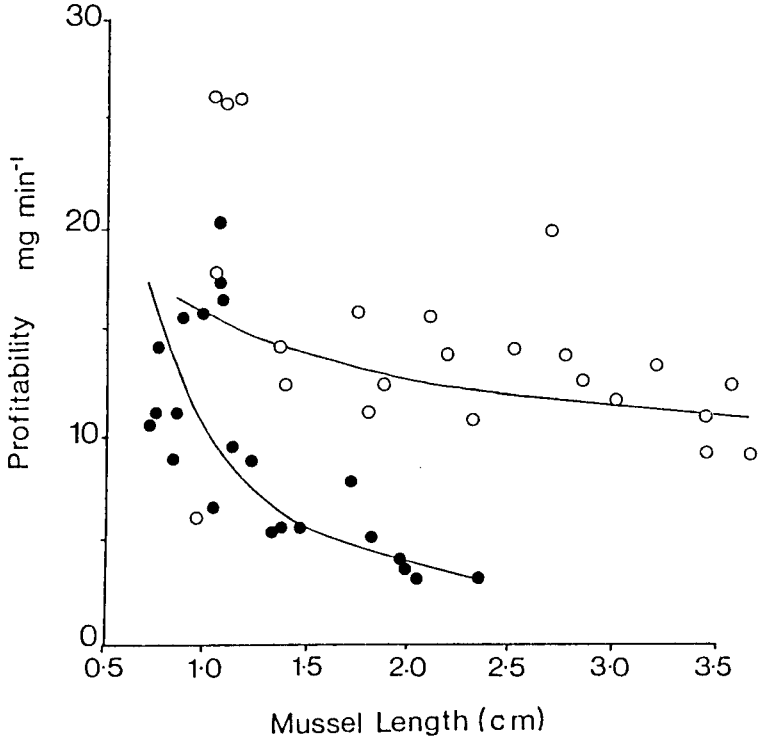


Fig.6 Profitability of Mytilus edulis aoteanas consumed by 2 size classes of Ovalipes catharus. Profitability curves derived from single regression of yield against prey size, fitted by power functions: • Crabs 50–55mm, $Y = 1.696X^{-1.44}$ o Crabs 80–85mm, $Y = 1.23X^{-0.29}$

Handling operations were not recorded for very large prey (>3.5cm), as these were consistently rejected by crabs, often after long periods. These data if included, would increase handling time slopes of large crabs closer to those recorded for small crabs.

Profitability

As prey length increased, profitability decreased monotonically (Fig.6). Analyses of regression lines for small and large crabs using log transformed data of profitability against log mussel size revealed significantly different slopes ($F(profit) = 16.91$, $df = 1:43$, $P < .001$) and intercepts ($F(profit) = 48.71$, $df = 1:43$, $P < .001$). Larger crabs with therefore stronger chelae had higher elevations reflecting their shorter handling times. Crabs which selected small bivalves (<1.0cm) gained the highest energy yields because of their ability to handle these prey in a shorter time. The high slope value of -1.44 for small crabs indicated a rapid decline in profitability with increasing mussel size. This contrasted strongly with large crabs where a profitability slope of -0.29 indicated relatively little decrease in profitability with increasing mussel size.

Equal Ratio Experiments

When presented with six size categories of potential prey items there was individual variability both between crabs of the same size and for individual crabs from day to day. However, the combined data revealed a clear foraging pattern (Fig.7). The percentage of prey consumed increased to a maximum value regarded as the most preferred prey category. For small crabs between 1.0 and 1.5cm length and for large crabs, 1.5 and 2.0cm. Above these values the percentage of prey consumed declined as prey size

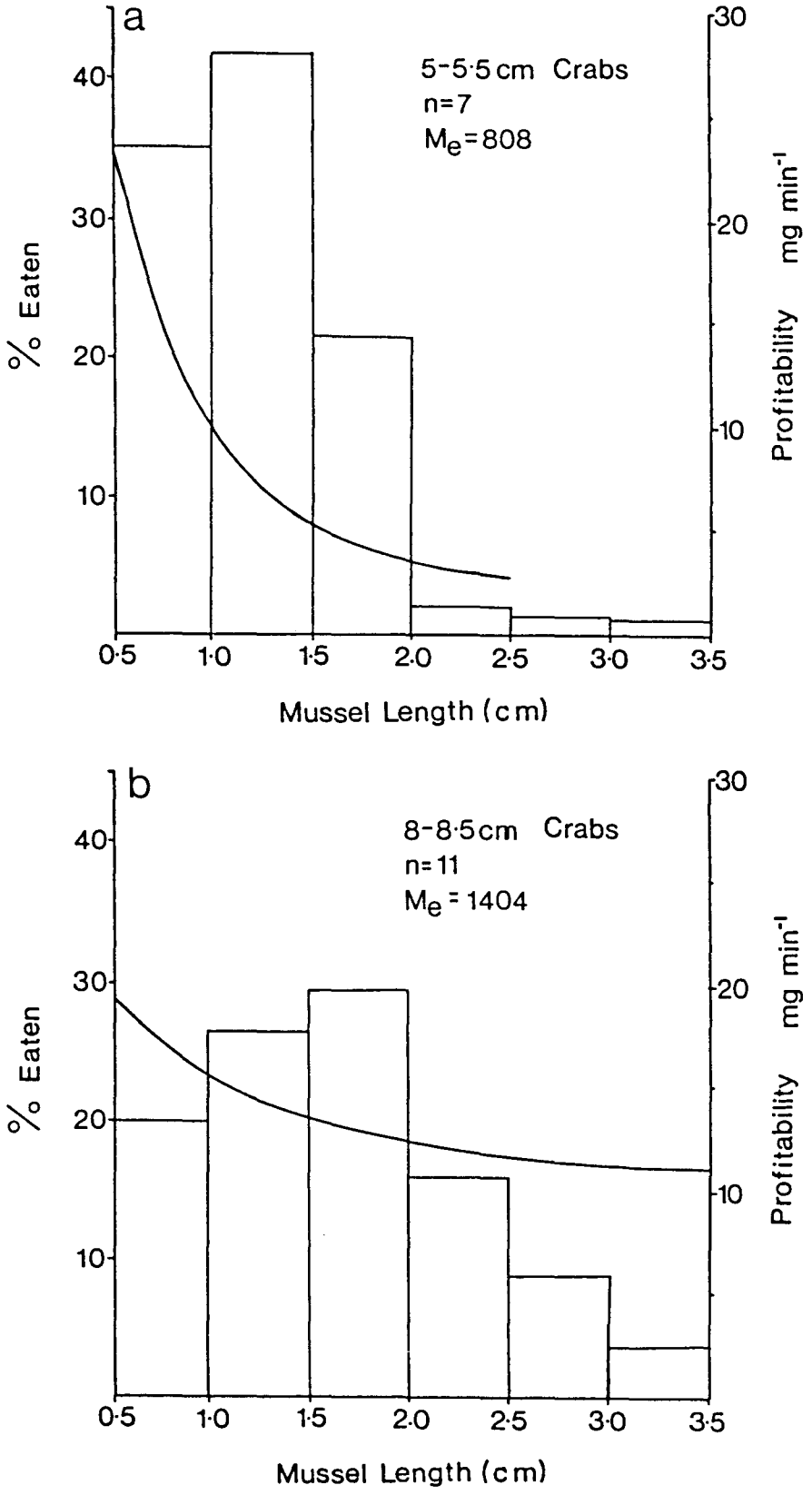


Fig.7. Percentage of mussels consumed over 12 days under constant prey availability by two crab size categories (a) 50–55mm and (b) 80–85mm Me = total number of mussels eaten. Profitability curves fitted by power functions (a) $Y = 1.696X^{-1.44}$ and (b) $Y = 1.23X^{-0.29}$.

increased. As expected, the largest least profitable mussel categories were seldom eaten even though they could eventually be opened by all but the smallest crabs. However, both sizes of predator consumed less smaller more profitable prey than predicted on energy maximization grounds.

Paired Ratio Experiments

When large crabs encountered either small (0.5-1.0cm) or medium (1.5-2.0cm) mussels they were always consumed (Table I). Encounter levels with small and medium prey were, however, not accurately predicted by either the numbers present or from total prey surface areas (ln Mussel Surface Area = 1.87 ln Mussel Length - 0.44; Jubb et. al., 1983). Large mussels (2.5-3.5cm) were not always consumed when encountered. An increase in the encounter rates with large mussels corresponded with their increased availability. High rejection rates for large mussels, however, resulted in a higher than expected consumption of medium mussels. These were rarely encountered when their ratios dropped below the 1 medium : 5 large mussel level (Table Ib).

Prey profitabilities calculated for individual mussels presented to crabs (Fig.6) differed from prey profitabilities calculated from ratio experiments (Table 2). Profit (mg.min-') did not remain fixed but altered with the relative number of prey available. As encounter levels with smaller mussels increased, a corresponding rise in profitability occurred from 12.9 mg.min-' towards the predicted level of 19 mg.min-' (Table 2a). Large mussel profitability also increased with encounter level, rising from the predicted level of 16.6 mg.min-' to 20.2 mg.min-', the highest level recorded for any mussel category. These results suggest a relationship between encounter level, prey proportionality, handling times and thus energy returns to the

a)

Ratio	Enccunter level (Small prey)	Expected encounter level (Small prey) No.*	SA*	Proportion of eaten prey from the small category	Proportion of total prey handled but rejected (Small prey)	(Medium prey)
5:5	.32	.50	.17	.32	0	0
5:10	.37	.67	.29	.38	.02	.06
5:20	.56	.80	.45	.57	.05	.05

b)

Ratio	Enccunter level (Medium prey)	Expected encounter level (Medium prey) No.*	SA.*	Proportion of eaten prey from the medium category	Proportion of total prey handled but rejected (Medium prey)	(Large prey)
5:5	.30	.50	.23	.65	.02	.55
5:10	.22	.33	.17	.55	.01	.62
5:20	.06	.20	.10	.14	.01	.65

* Expected encounter levels predicted by numbers available (No.) and total surface areas (SA.): log y = 1.87 log x - 0.44, n = 94, r^2 = 0.99 (Jubb et al., 1983).

Table.I. Results of paired ratio experiments for (a) small (0.5–1.0cm) with medium (1.5–2.0cm) mussels, n = 170 and (b) medium with large (2.5–3.0cm) mussels, n = 150.

a)

Ratio	Encounter level (Small prey)	Profitability without rejection (mg min^{-1}) (Small prey)	(Medium prey)	Profit with rejection times (Small prey)	(Medium prey)
5:5	.32	12.9	15.2	12.9	15.2
5:10	.37	15.1	15.1	15.1	15.0
5:20	.56	19.7	15.6	18.1	15.3
Expected		19.1	13.9		

b)

Ratio	Encounter level (Medium prey)	Profitability without rejection (mg min^{-1}) (Medium prey)	(Large prey)	Profit with rejection times (Medium prey)	(Large prey)
5:5	.30	14.5	16.6	14.5	13.4
5:10	.22	14.2	18.4	14.2	16.5
5:20	.06	14.9	20.4	14.7	18.1
Expected		13.9	12.0		

Table. 2. Profitabilities (mg.min-') from paired ratio experiments both with and without the inclusion of rejection times, a) medium (1.5-2.0cm) with small (0.5-1.0cm) mussel sizes and b) medium (1.5-2.0cm) with large (2.5-3.0cm) mussel sizes.

predator.

Observatiors made on crabs during ratio experiments showed that large mussels would often be manipulated longer than the time required for immediate rejection (stated by Elner and Hughes (1978) as 1-4 seconds for Carcinus maenas). Handling times for large mussels are included in Table 3. Rejection within 1-4 seconds of 14% of all large mussels suggests an almost immediate recognition of these prey as unprofitable. A further 42.9% were manipulated for up to 30 seconds during which time mussels were presumably tested for vulnerability. The remaining 17.5% of prey rejected were attacked using a wide range of opening techniques for up to 7 minutes. Of the total, 25.6% were successfully opened yielding high energy returns (Table 2). This prolonged attention period on 85.9% of large prey suggests that crabs recognise some factor of mussel vulnerability warranting further attack.

Further breakdown of rejection times for large mussels (Table 4), shows that as the number of these prey handled increased there was a decline in average assessment time. The number of large prey immediately rejected (1-4sec) was greatest when, for every 2.2 medium mussels 7.8 large prey were encountered (5:10 ratio). Consequently, more mussels were handled per unit time, increasing the chance of an encounter with the medium prey. When encounter rates with large prey reached 94%, the number immediately rejected declined and the number assessed increased. At this level the highest number of large prey were successfully opened (Table Ib).

Prey Abundance

Differences in crab foraging behaviour associated with mussel abundance were

Event	Description	Time Involved	Number	Percentage of Total mussels handled
Initial assessment	Immediate rejection	1 - 4 sec	45	14.1
Vulnerability assessment	Use of 1 occasionally 2 opening techniques involving slight manipulation-prey rejected	5 - 30 sec	137	42.9
Serious attack	Mussel accepted Use of a series of opening techniques ending in eventual failure and rejection	0.5 - 7 min	56	17.5
Successful attack	Mussel opened following a period of prolonged attack	-	81	25.6

Table. 3 . Analysis of rejection times for *O. catharus* presented with large (2.5–3.0cm) *M. edulis aoteanus* .

Ratio*	Encounter level (large prey)	Immediate Rejection 0-4 sec		Vulnerability assessment 5-30 sec		Serious attack 30 sec +		Successful attack		% large prey opened from total handled
		n	x	n	x	n	x	n	x	
5:5	.70	11	3.0	30	17.4	21	95.3	17	613.1	21.5
5:10	.78	26	3.0	44	12.6	10	72.1	22	552.1	21.6
5:20	.94	7	3.0	64	12.5	22	86.1	42	505.1	31.1

* Ratios represent numbers of mussels presented, medium (1.5-2.0 cm): large (2.5-3.0 cm).

Table. 4 . Analysis of large mussel handling times and numbers for *O. catharus* presented large (2.5-3.0cm) with medium (1.5-2.0cm) *Mytilus edulis aoteanus* .

observed. Mussels presented individually were seldom rejected and the shell fragments cleaned of all the flesh. When mussels were presented in groups, crabs would often hold 2 prey, 1 in each chela, and attempt to open 1 of these prey using the mouth parts for support. This reduced handling efficiency, resulted in increased handling times. Mussel grouping also influenced the degree of flesh consumption as crabs would often leave a small portion of difficult to access meat. This resulted in depressed handling times and is possibly an important factor contributing towards the observed increase of profitabilities with mussel abundance (Table 2).

DISCUSSION

Size selection in *O. catharus* feeding on mussels was shown to depend upon many factors including predator size, prey size, vulnerability and availability. Crabs were able to open mussels using 5 techniques and generally utilized a characteristic attack sequence. This allowed a wide range of prey sizes to be opened including very small and large mussels. The methods used by *O. catharus* are similar to those used by other crabs of the family Portunidae including *Carcinus maenas*, *Liocarcinus puber*, *Callinectes sapidus* and *Ovalipes punctatus* (Elner, 1978; Hughes and Seed, 1981; Du Preez, 1984; Rheinallt, 1986). However, in comparison with these other portunid crabs, *O. catharus* consistently manipulated and ate mussels of a smaller size (<1.0cm length). This ability was shown to be an important influence on its predatory efficiency.

O. catharus like other portunid crabs exhibits active prey selection behaviour. Such selection is likely to be influenced by morphological features of the feeding apparatus, chelipeds, mouthparts, walking limbs and the overall size of the predator (Davidson and Marsden, In Press). *O. catharus* like many molluscivorous crabs (Vermeij, 1977) possesses dimorphic chelipeds: a robust crusher with a large proximinal tooth and a smaller cutter chela, bearing sharp conical teeth on each finger. Strength is related to cheliped size, shape, location of the occlusive surfaces, symmetry of occlusive pairs, degree of closure between opposing surfaces and alignment of forces at the point of force delivery (Elner, 1978; Brown, et al., 1979; Boulcing, 1984). Therefore, preferred prey size is likely to be a function of the crabs chelae. Small individuals of *O. catharus*, *C. maenas* and *C. sapidus* have preference for *Mytilus* spp. of similar length, however, large *O. catharus* preferred a smaller prey size than *C. maenas*,

L. puber and C. sapidus . C. maenas and L. puber have large chelipeds with blunt dactyli and are able to open larger mussels than the two swimming crabs possessing relatively long and slender chelipeds, with dactyli extending nearly half the length of the propi. Elner and Hughes (1978) also reported the disadvantages of large cheliped size in that some large C. maenas mis-handled or dropped smaller mussels, a phenomenon also recorded by Rheinallt and Hughes (1985) and Rheinallt (1986) for L. puber feeding on Mytilus . Small prey were handled more efficiently by the finer chelipeds of O. catharus with more slenderly tapered dactyli. The shape and size of the chelipeds appear to explain the different handling times and thus profitability curves calculated for these crabs feeding on mussels. For O. catharus and C. sapidus , profitability curves are monotonic decreasing from high values for small prey sizes (0.5-1.0cm), to low values for larger prey sizes. This contrasts with C. maenas and L. puber where the profitability curve had a maximal value for medium size prey and reduced profitability for small and large prey.

Lawton and Hughes (1985) suggested that profitability curves derived from single regressions of yield and of handling time on prey, failed to predict profitability accurately. By fitting separate handling time functions above and below the critical prey size, the authors were able to predict profit more accurately. O. catharus opening time curves suggest that a critical prey size exists, above which a second, slower opening method was adopted by crabs. However, profitabilities calculated using individual handling times for both small and large crabs showed no indication of a profit peak at or near the critical prey size. Therefore, the use of 1 equation for O. catharus feeding on mussels adequately describes profitability against prey size.

The foraging behaviour of individual portunid crabs is regarded as variable (Elner, 1980; Hughes and Seed, 1981) and some authors have suggested that factors such as learning, past experience and prey size may be responsible (Hughes, 1979; Hughes and Elner, 1979; Jubb et.al., 1983; Cunningham and Hughes, 1984). However, the attack pattern adopted by portunid crabs feeding on particular prey generally remains consistent. O. catharus appeared able to recognise mussel size, thus the strength and adopted an appropriate attack strategy. But, whether this recognition-assessment is based on the relative strengths of stimuli from the grasped mussels (Jubb et.al.,1983) prior to attack or gained once attempts to open the mussel were initiated is uncertain. Analysis of rejection times for O. catharus feeding on large prey suggested that some assessment occurred during opening attempts. The immediate rejection of 14% of all large prey handled suggests that O. catharus is able to recognise some prey as unworthy of further attention.

When presented with combinations of various prey sizes O. catharus like C. maenas (Elner and Hughes, 1978; Jubb et. al., 1983), L. puber (Rheinallt, 1986), C. sapidus (Hughes and Seed, 1981), Scylla serrata (Hill, 1979) and O. punctatus (Du Preez, 1984) all selected prey of a certain size. Small and medium mussels were almost always accepted while most large mussels were rejected. Optimal foraging theory (Pyke,et al., 1977; Hughes, 1980) predicts tha for a predator like O. catharus greatest predation should occur on prey categories which yield the highest energy return per unit foraging time (ie.small mussels <1.0cm). The unexpected selection by swimming crabs of less profitable mussels is best explained by low encounter rates and misidentification of the smallest prey. These prey were seldom dropped or mishandled, however, crabs would often fail to recognise them amongst shell debris of previously opened or larger mussels.

Simple foraging strategy predictions (Estabrook and Dunham, 1976; Lehman, 1976) often assume that handling times and thus profitabilities remain constant. This was true for O. catharus feeding on medium mussels. Recent studies have recognised, however, that the time taken to handle food may be influenced by factors including prey encounter rates, hunger, forager experience and the development of a search image by the predator (Werner, 1974; Calow, 1975; Cornell, 1976; Kislalioglu and Gibson, 1976; Hughes, 1979; Palmer, 1981; McNair, 1981, 1982; Cunningham and Hughes, 1984; Pyke, 1984). Handling times for O. catharus feeding on mussels did not remain constant but declined when paddle crabs encountered small and large mussels more often. Increased encounters with these difficult to handle prey probably increases forager experience resulting in greater handling efficiency. The reduction in handling times may increase profitability of a particular sized prey sufficiently to outrank a previously higher ranked prey (Hughes, 1979). For O. catharus , increased encounter rates and reduced handling times when feeding on large mussels resulted in the transposition of large over the medium sized prey.

Reduction of handling times for C. maenas has been attributed to its ability to learn (Cunningham and Hughes, 1984) and this study suggests that O. catharus also has this ability. It should be noted, however, that some decrease of handling times was due to discarding of larger mussels before all the flesh had been removed. This incomplete consumption occurred only when mussels were presented in groups, suggesting a rejection response initiated by the presence or physical contact with other mussels, as proposed by the relative-stimulus hypothesis of Jubb et.al.(1983). Blundon and Kennedy(1982a) found that C. sapidus showed no prey selectivity and opened all sizes of clams when encountered separately. For O. catharus , the abundance and presumably the number of physical contacts with large

mussels, resulted in increased rejection rates (55 to 65%). These results suggest that increased crab selectivity may be a response to prey abundance and the simultaneous contacts with other prey. This may also be influenced by search time, the period between contact with successive prey and the degree of effort required to obtain the prey item. This would become significant for bivalves which burrow deeper with increasing size.

Relative abundance of food types has already lead to modified predictions of the optimal diet model (Cornell, 1976). Hughes (1979) suggested that as the abundance of a more valuable food type decreases the forager first specialize on the more valuable food type, may then generalize, and finally specialize on the less valuable food type. Paired ratio experiments on O. catharus suggest that a similar switching pattern occurs. However, examination of rejection times for large mussels shows that, as the abundance of medium mussels declined, crabs rejected more large mussels immediately. Instead of generalizing on both sizes of mussel O. catharus continued to specialize on medium sized prey. As the abundance of larger mussels was further increased the number immediately rejected decreased. As a consequence, the number assessed and successfully opened increased to 94.6% of all prey opened. It appears that relative abundances become an important factor in prey selection when there are significant rejection times. Results suggest, large unprofitable mussels would only be eaten when prey are scarce or encountered infrequently. This may also result in predation on the weaker or more vulnerable individuals within a size class. This process would be further influenced by predator experience whereby the predator is likely to assess food types they have encountered before (Cornell, 1976).

In discussing the ecological implcations of prey selection Hughes and Seed

(1981) suggested that handling times for C. sapidus were modified to minimize time and thus exposure to predation by birds. O. catharus normally occupies subtidal temporary burrows (McLay and Osborne, 1985) and is predated by fish (Mitchell, 1984). When feeding, paddle crabs stay on the surface and appear less sensitive to visual stimuli. Therefore, time spent feeding increases the risk of predator attack. The preference by paddle crabs of small prey minimizes time at risk and also maximizes energy intake under this constraint.

It is suggested that O. catharus is capable of developing a flexible search image. The acceptance or rejection of prey in response to prey contact and encounter rate, the reduction of handling times, the vulnerability assessment of large prey, prey switching and the discarding of unfinished mussels shows that these crabs are able to modify foraging behaviour. This has probably evolved in response to prey characteristics, including distribution, density, size, vulnerability and availability of other prey. The flexible foraging strategy enables O. catharus to feed on each patchily distributed prey type encountered while simultaneously maximizing energy intake and minimizing time expenditure.

SUMMARY

Paddle crabs Ovalipes catharus (White, 1843) adopt 5 distinct opening techniques when feeding on the blue mussel Mytilus edulis aoteanus Powell in the laboratory. The particular opening technique used is influenced by bivalve size. Small mussels, less than 1.0cm length are quickly crushed by the chelae and/or mandibles, while mussels between 1.0 and 3.0cm are crushed across the umbone area or over the adductor muscle. Larger or more robust prey are opened slowly by wedging into, or chipping the shell until the minor chela gains access and is able to cut the adductor muscle. Handling times increased exponentially with mussel size, and resulted in a regular decrease in profitability (yield of flesh per unit handling time). Prey selection experiments using equal ratios of mussels within the size range 0.5-3.0cm length, showed that large and small crabs preferred a medium size prey. The preferred prey length increased with predator size, 1.0-1.5cm for small crabs and 1.5-2.0cm length for large crabs. Paired ratio experiments suggested the smallest mussels (0.5-1.0cm) suffered reduced predation as they were often misidentified or obscured among the larger prey. Declining predation pressure on large mussels (2.5-3.0cm) is the result of high rejection rates. Analyses of rejection times showed that 81% of larger prey were not rejected immediately, but handled further for periods up to 7 minutes. As encounter rates with small and large prey increased, handling times declined. The improvement of handling times suggests that O. catharus is able to learn or gain information by experience about the prey. This is the basis of a flexible search image, evidence of this foraging strategy are discussed.

IMPROVEMENT OF PREDATORY EFFICIENCY

BY THE

PADDLE CRAB *Ovalipes catharus*

FEEDING ON THE BLUE MUSSEL,

Mytilus edulis aoteanus

Key Words: Optimal Foraging, Learning, Predator-Prey, *Ovalipes*, Handling Times

INTRODUCTION

The selection of prey by invertebrate predators is affected by many factors including detectability, vulnerability, energy content and previous exposure to that prey. Prey selectivity in crabs, according to Hughes (1980) may reflect either passive mechanical or active behavioural mechanisms of choice. For portunid crabs, including Ovalipes catharus,(Davidson, 1986), there is considerable evidence for size selection based on active behavioural methods (Cunningham and Hughes, 1984; Hughes and Seed, 1981; Jubb et al., 1983; Lawton and Hughes, 1985). Most of the studies suggest that crabs 'recognise' optimal prey by various means including tactile stimuli from the pereiopods independent of manipulation by chelae or mouthparts.

The basis for such recognition,however,has not been fully identified. For the velvet swimming crab, Liocarcinus puber, ap Rheinallt (1986) suggested mechanical factors related to the ability of the crab to manipulate prey may be responsible. Prey recognition as a means to optimise food intake however, not only depends upon the ability of the predator to select prey, but to learn by experience and retain the knowledge.
Cunningham and Hughes (1984) showed learning of predatory skills by the common shore crab, Carcinus maenas. Following exposure to 5 or 6 consecutive mussels, crabs were found to reduce handling times by a factor of 0.3. These skills which were gained in a matter of hours were lost more slowly with partial retention persisting for at least 2d.

The role of learning in increasing predatory skills may not simply be restricted to reducing the number of attacks required to break open prey or reducing the time required for breaking the shell. Experience gained at eating prey following a successful attack may reduce eating time and therefore affect the profitability of consecutive prey items. This was a feature

predicted from the results of experiments conducted by Cunningham and Hughes (1984).

The present study was designed to investigate the possible increase in predatory skill by Ovalipes catharus feeding on optimal prey (mussel, Mytilus edulis aoteanus of length 2cm). It compares attack methods, opening and eating times of crabs without previous exposure to mussel prey with those experienced at opening mussels. It may therefore provide behavioural explanations for predatory behaviour and confirm the potential for prey items to become transposed in rank.

MATERIALS AND METHODS

Ovalipes catharus (White) were captured by trawling from Brighton Beach, Canterbury and blue mussels, Mytilus edulis aoteanus Powell collected from the upper mid-tidal zone of an exposed shore situation. This standardized shell characteristics, which may vary with exposure and tidal level (Seed, 1980). Mussels were used within two days of collection to ensure freshness, with damaged or individuals in poor condition being discarded. Only male crabs, 75 to 90mm carapace width were used in experiments to avoid potential bias which may be caused by sexual differences in morphology or predatory behaviour. Crabs used in experiments were unlikely to have had previous exposure to the bivalves used in the learning experiments. Crabs were kept individually in glass aquaria (60 x 30cm) filled to a depth of 40cm with closed circuit running seawater at 18°C.

Paddle crabs were conditioned to one of two feeding treatments prior to further experimentation. Eight freshly collected Ovalipes catharus were fed on mussel flesh for three days (naive crabs), while another eight crabs were allowed to feed freely on whole mussels (0.5-3.0cm) for three days (experienced crabs). During the preconditioning sequence all crabs consumed similar quantities of mussel flesh. Following three days starvation, all crabs were presented with individual whole mussels of length 2cm. The size of mussel used in learning experiments was selected from the preferred size category, determined from previous experiments. Opening time (time from the first physical contact to the first bite of flesh), and eating time (from first bite through flesh consumption to the rejection of the last piece of shell) were measured for each prey presented. The opening techniques were recorded and the frequency and success on each individual mussel recorded. Five mussels were presented to crabs consecutively over a time period between 0.5 and 1 h.

RESULTS

Paddle crabs used four recognisable techniques to attack and open 2.0cm length blue mussels in the laboratory: a) anterior or umbone crushing, used in 52.3% of attacks, successful on 75% of all opened mussels; b) posterior crushing, used in 40.5% of attacks and successful 17.5%; c) wedging, used in 6.3% of attacks, successful for 7.5% of prey opened and d) chipping, used for 0.9% of attacks but never successfully (Table 5). The frequencies with which crabs used these techniques to open mussels, and the opening success rate did not differ significantly between crab treatments ($H = 0.04$; $P = 0.6723$).

Mean time taken by naive crabs to handle five successive mussels declined by a factor of 0.54 for opening time (Fig. 8) and 0.27 for eating time (Fig. 9). Prey handling times for experienced crabs fed freely on mussels three days prior to experiments, declined by 0.67 for opening time and 0.34 for eating time. Comparison of eating times showed that experienced crabs improved by 0.30 compared with naive crabs ($F = 14.29$; d.f. = 1,72; $p < 0.001$) (Table 6). Opening times recorded by naive and experienced paddle crabs attacking mussels, were not significantly different ($F(slope) = 0.29$; d.f. = 1,69; $P > 0.5$) ($F(intercept) = 0.13$; d.f. = 1,69; $P > 0.5$), however, the opening time reduction between the first and second mussel was greater for experienced crabs. Naive crabs became experienced at opening mussels following manipulation of about 2 mussels. Previously experienced crabs required only one mussel to regain optimal techniques.

The mean number of attacks required to open mussels, irrespective of the technique, decreased from approximately 3.9 to 1.7 for naive crabs and approximately 3.3 to 1.3 for experienced crabs after five mussels (Fig. 10). No significant difference in the number of attacks required to open prey was recorded between crab treatments ($F(slope) = 0.0001$, d.f. = 1,71; $P > 0.75$),

(F(intercept) = 0.6; d.f. = 1,71; P > 0.25).

Profitability, defined as dry weight of mussel (mg) / handling time (min) (Hughes and Seed, 1981) increased as crabs encountered consecutive prey items (Fig. 11). Profitabilities increased from 11.7 to 15.7 mg/min^{-1} for naive crabs and 12.2 to 18.6 mg/min^{-1} for experienced crabs. The rate of profit increase did not differ between crab treatments (F(slope) = 0.055; d.f. = 1.72; P>0.75) (Table 6). Profits gained by experienced crabs, however, were significantly higher (F(intercept) = 10.05; d.f. = 1,72; P < 0.005) than profits for naive crabs. This result was due to shorter overall eating times for experienced compared with naive paddle crabs.

Table 5 Application and success rates of the four techniques used by *Ovalipes catharus* to open *Mytilus edulis aoteanus*.

	NAIVE CRABS				EXPERIENCED CRABS			
	Anterior	Posterior	Wedging	Chipping	Anterior	Posterior	Wedging	Chipping
Percent employed	52.3	40.5	6.3	0.9	53.6	42.0	4.3	0
Percent successful	75.0	17.5	7.5	0	74.3	22.9	2.9	0

Table 6 Comparison of regression lines for naive and experienced Ovalipes catharus in learning experiments.

Comparison	Group	Regression equation	Slope	F. Statistic	dif.	Significance
Opening Times	Naive	log Y = 10.26 - 2.49 log X	-4.49	Slope = 0.29	1,69	NS
	Experienced	log Y = 8.30 - 1.70 log X	-1.70	Intercept = 0.13	1,69	NS
Eating Times	Naive	log Y = 8.26 - 0.96 log X	-0.96	Slope = 0.2	1,72	NS
	Experienced	log Y = 8.86 - 1.33 log X	-1.33	Intercept = 14.29	1,72	**
Profit	Naive	log Y = 1.13 + 0.77 log X	0.77	Slope = 0.055	1,72	NS
	Experienced	log Y = 1.0 + 0.89 log X	0.89	Intercept = 10.05	1,72	*

* Significant at 0.005 level, ** Significant at 0.001 level.

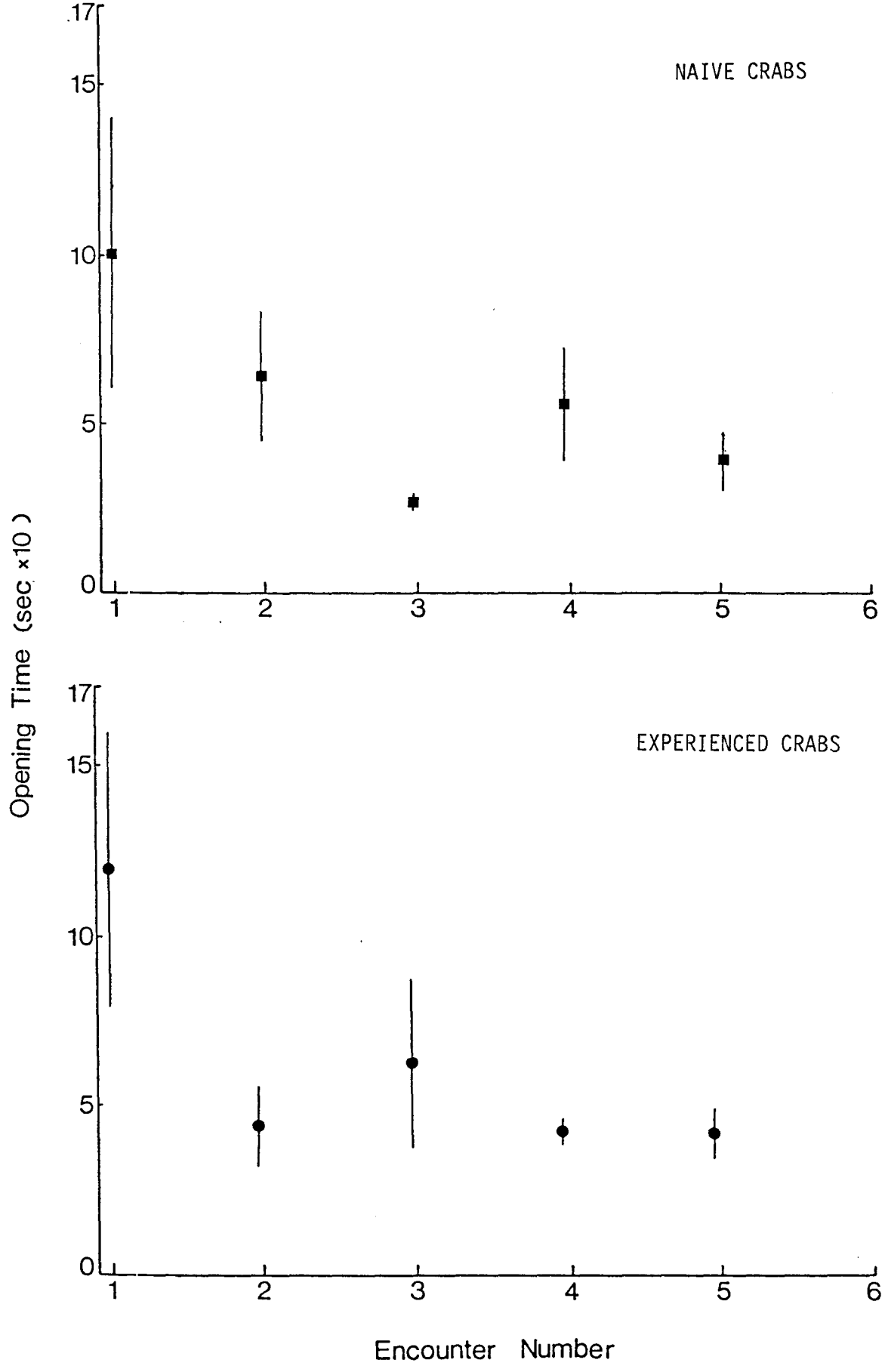


Fig. 8. Mean opening times for naive and experienced Ovalipes catharus, presented with successive mussels Mytilus edulis aoteanus. Error bars represent 95% confidence intervals.

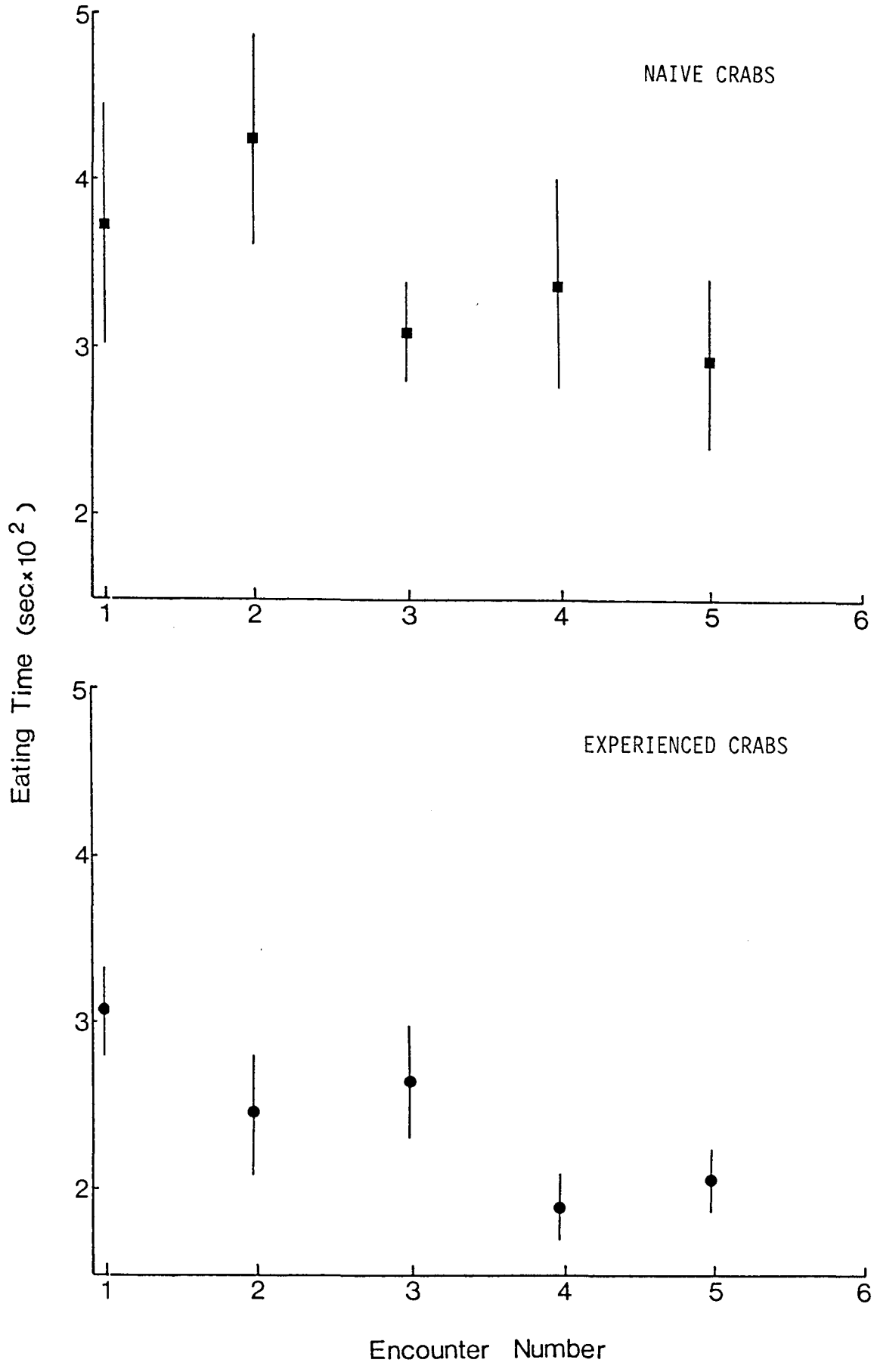


Fig. 9. Mean eating times for naive and experienced Ovalipes catharus, presented with successive mussels Mytilus edulis aoteanus. Error bars represent 95% confidence intervals.

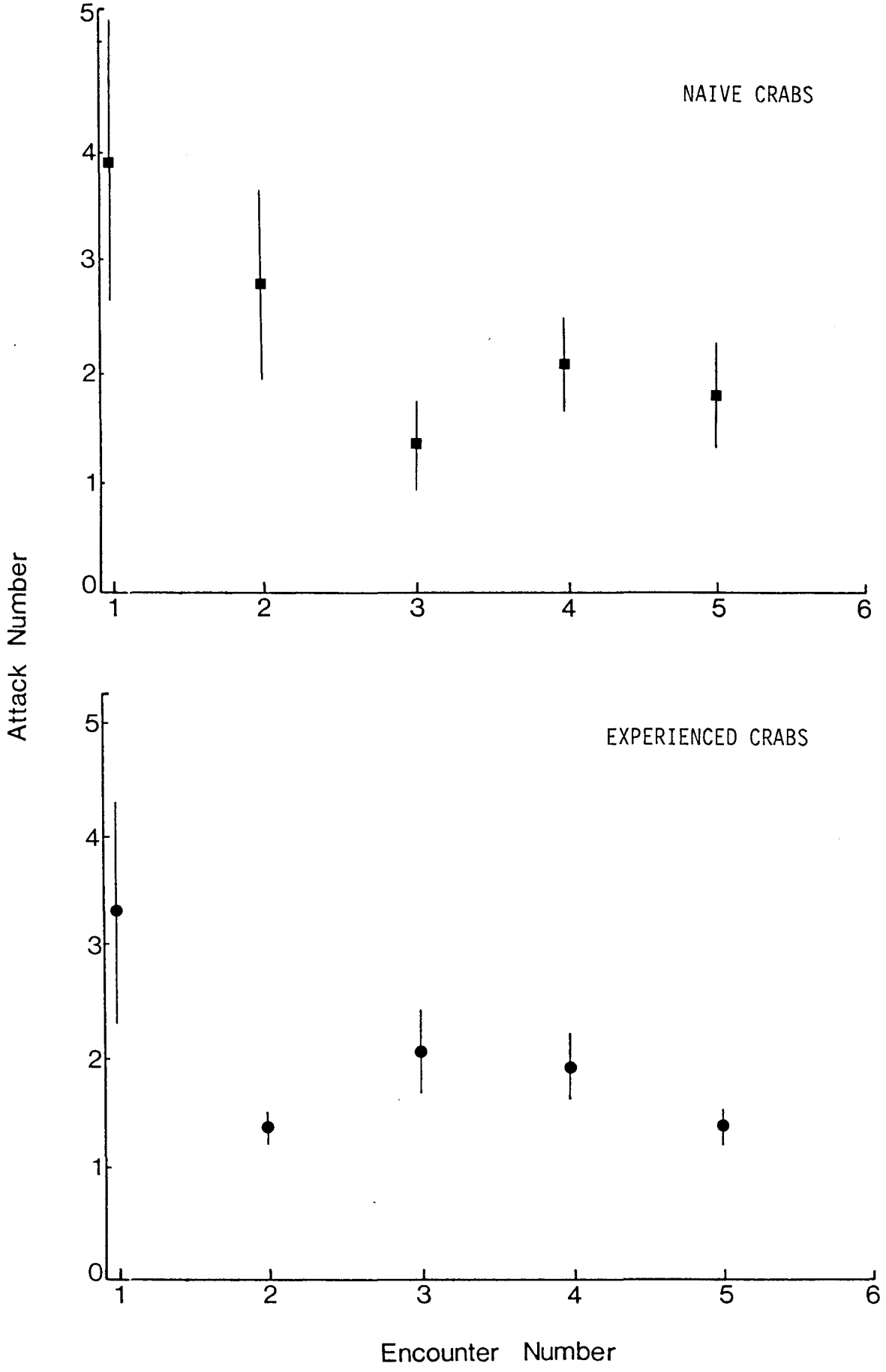


Fig. 10. Mean number of attacks reqired by Ovalipes catharus to open successive mussels Mytilus edulis aoteanus. Error bars represent 95% confidence intervals.

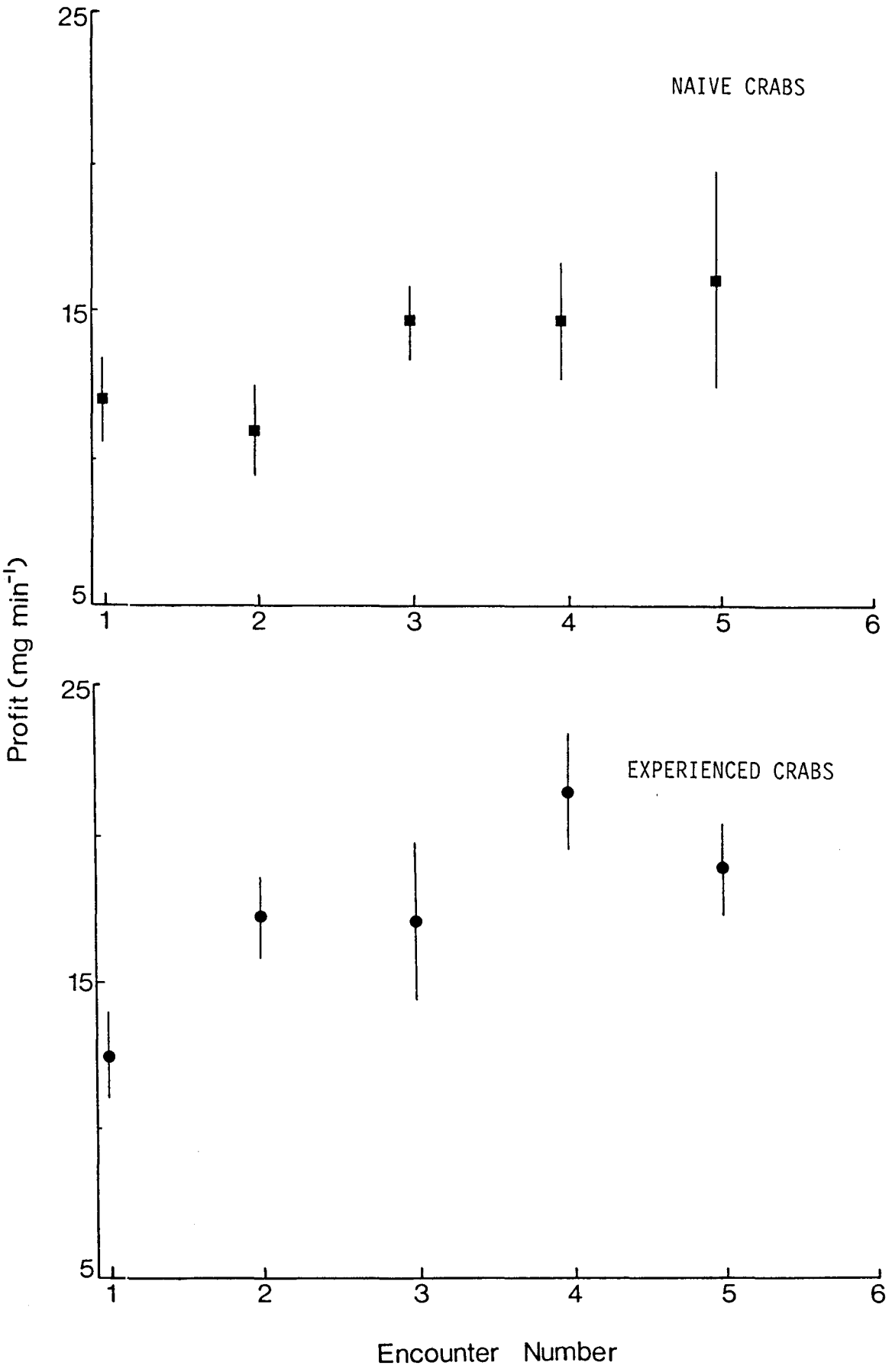


Fig. 11. Mean profitability of consecutive mussels Mytilus edulis aoteanus presented to Ovalipes catharus. Profit calculated as mussel flesh (mg) / handling time (min). Error bars represent 95% confidence intervals

DISCUSSION

During learning experiments *O. catharus* utilized 4 of the mussel opening techniques previously described for this species. The one method not used on mussels of 2cm length was outright crushing by the mouthparts or chelae. Such opening methods of *O. catharus* are consistent with those reported for many other portunid crabs (Elner, 1978; Elner and Hughes, 1978; Hughes and Seed, 1981; Cunningham and Hughes, 1984; ap Rheinallt and Hughes, 1985; Choy, 1986). For *O. catharus*, as in *C. maenas* (Cunningham and Hughes, 1984), crushing at the umbone region of the mussel was the most common form of attack and resulted in the highest success rate. This is probably related to the shape of the mussel shell, the umbone region is more easily held and the chela can gain greater mechanical advantage. *O. catharus*, however, used the less successful posterior crushing in combination with anterior crushing. The advantage of this behaviour may be to detect weak spots in the posterior part of the shell. Crushing this area resulted in more shell damage than anterior crushing and as a consequence, crabs were able to glean tissue more efficiently resulting in faster eating times. Wedging and chipping techniques were used only after attempts to open mussels by anterior or posterior crushing had failed. Although wedging and chipping were seldom successful, mussels were sufficiently weakened for subsequent crushing techniques to succeed.

For *O. catharus*, the same opening techniques were used by naive crabs and those experienced at opening mussels. The frequency with which particular techniques were used was similar in both groups but the success rate differed significantly. As naive crabs became more experienced at handling mussels, both the number of attacks required to open them decreased and associated with this was a reduction in opening time by a factor of 0.54. Such rapid improvement in efficiency following handling of only 3 mussels is far greater than that

recorded for C. maenas, where the value was 0.3 after consumption of 5 to 6 prey items (Cunningham and Hughes, 1984). O. catharus previously exposed to mussel prey regained full predatory skills following handling a single prey item. As experience at opening mussels was gained quickly, the overall opening times for naive and experienced crabs were similar.

Following opening of 5 consecutive prey, the eating time for inexperienced O. catharus feeding on mussels decreased by a factor of 0.27. However, the time required to consume the flesh was approximately a third longer than experienced crabs. It may be postulated that these differences may be a consequence of the preconditioning feeding regime. However, the starvation period used in the present experiments was similar or greater than that used in other studies where it has been necessary to standardise hunger levels (Jubb et al., 1983; Lawton and Hughes, 1985; ap Rehinallt and Hughes, 1985). O. catharus with 3 days experience at opening mussels, followed by 3 days without physical contact with mussels retained partial retention of eating skills and eating times continued to decrease throughout the experimental period. In contrast with opening times, which are rapidly learnt it appears the improvement of eating proficiency required more encounters with prey.

From the results of their learning experiments on C. maenas, Cunningham and Hughes (1984) predicted an increase in the profitability of consecutive prey items eaten. The curve calculated for both dogwhelk and mussel prey predicts a rapid increase to maximal values following ingestion of about 3 or 4 prey items. In these calculations the authors assumed that eating time remained constant, a feature inconsistent with the present study. For O. catharus the rate of profitability increase over the 5 prey items consumed was similar for naive and experienced crabs feeding on mussels. However, the overall improvement in profitability following learning resulted in increases

from 11.7mg.min^{-1} to 18.6mg.min^{-1} representing an approximate increase of 60%. Such potential increases in profitabilities would favour an optimally foraging predator which switches its specialised diet either from one prey to another or onto a different size class of the same prey.

Most portunid crabs are regarded as opportunistic omnivores with a preference for animal prey. In temperate regions the dietary composition of field collected crabs including O. catharus is composed of a wide range of items including small bivalves, crustacea and algae (Paul, 1981; Du Preez, 1981; Williams, 1982; Choy, 1986; Wear et al., in press). These contrast with some cancrid crabs and molluscs which specialise on molluscan prey, often removing considerable numbers from commercial shellfish beds (Hancock, 1960; Muntz et al., 1965; Holland et al., 1980; Griffiths, 1981). Whelks such as the dogwhelk Nucella lapillus have complex predatory behaviour, show size selection based on previous experience and increase predatory efficiency when feeding on mussels. The learned behaviour, enabling the predator to drill in the thinnest part of the shell, increases the profitability of mussels less than 25mm in length by about 17%. The authors concluded that increased profitability allowed dogwhelks to utilize prey smaller than that predicted from the size relationships alone. Directed drilling allowed rapid access to the most profitable tissue and shorter handling times possibly reduce the risk of predation or dislodgement during feeding.

For O. catharus it is difficult to assign such direct ecological advantages to the behavioural mechanisms described here. Switching behaviour and the development of a flexible search image (Cornell, 1976) is characteristically associated with predators which feed on food which is clumped or patchy in distribution. Naturally-occurring patches, however, vary in composition quality and may change with time of day or season. Such food resources therefore require a flexible predatory strategy. O. catharus is

able to learn and retain prey characteristics sufficiently to improve handling efficiency on prey. As a number of techniques are utilised it seems likely this could be applied to a range of potential bivalve prey found in the habitat.

The potential for improvement in predatory efficiency by crabs probably depends upon two main factors. Firstly, the learning ability as demonstrated here and secondly, the mechanical limits of the feeding apparatus. Chelal morphology determines not only the strength of forces generated during crushing (Vermeij, 1977) but also affects dexterity. Within the portunids there is considerable variation in the way in which mussels of a similar size were manipulated, broken and eaten. Ap Rheinallt and Hughes (1985) have suggeste that the chelal morphology of the velvet swimming crab is more suited to mobile crustacean rather than mollusc prey. However, male Liocarcinus puber (ap Rheinallt and Hughes, 1985) and O. catharus (this study) break small mussels faster than C. maenas of a similar size (Elner and Hughes, 1978). In comparison, C. maenas also dropped small prey and was inefficient at gleaning flesh from the inside of the shell. Increased dexterity of the chelae of O. catharus probably increases markedly its ability to manipulate, break and consume mussels. These differences in chelal dexterity probably explain the increased predatory efficiencies and profitabilities found in this study compared with those recorded for C. maenas (Cunningham and Hughes, 1984).

For O. catharus, the improved handling and eating efficiencies demonstrated in this study potentially minimise feeding time and could increase the time available for searching. Learnt behaviour would be retained for periods greater than 3 days allowing exploitation of prey which may be irregularly distributed. Although there is little evidence to support this type of foraging behaviour from field studies I have nevertheless shown that O. catharus, a generalist predator possesses specialised behavioural mechanisms based on mechanical factors.

SUMMARY

Paddle crabs Ovalipes catharus (White) both with and without previous experience at opening mussels used the same 4 techniques to attack Mytilus edulis aoteanus in the laboratory. These were anterior and posterior crushing, wedging and chipping. Crabs employed anterior crushing most often (52.3%) resulting in the highest success rate (75%) of all the opening methods. Posterior crushing was used when anterior crushing failed (40.5%), but was successful for only 17.5% of all prey opened. The frequency with which each technique was used was similar in the two groups tested and did not change as crabs opened successive prey. The mean number of attacks required to open mussels, however, declined from 3.9 attacks for the first mussel to 1.3 attacks for the fifth mussel. Mean opening times decreased by a factor of 0.65, while eating times decreased by 0.27 after five prey had been attacked. Mussel opening times recorded for crabs previously experienced at handling mussels showed little further decline. Eating times, however, were reduced in experienced crabs by a further factor of 0.3. While opening efficiency was rapidly learned, reduction of eating times required more prey encounters.

Decreased handling and eating times with experience resulted in increased profitability for consecutive prey items. This fulfills the requirements which lead to prey switching behaviour. The improvement in predatory skills is discussed in relation to morphology, feeding characteristics and habitat of the crab.

CHAPTER II

THE BOTTOM FAUNA AND NATURAL FOOD OF THE PADDLE CRAB *Ovalipes catharus* FROM THREE CANTERBURY SOFT BOTTOMS

Key Words: *Ovalipes*, Index of Relative Importance, Predator-Prey, Diet, Benthos, Epibenthos

INTRODUCTION

In marine soft bottom communities, species are likely to interact in many ways including competition for food and space and predation. These communities are often complex and the direct effects of predation are often difficult to assess. Studies on community structure, suggest predators may be able to control and maintain prey densities (Virstein, 1977, 1979; Kelso, 1979; Holland et al., 1980; Blundon and Kennedy, 1982b). Other studies based on hard shore communities maintain that predation also acts to increase species diversity on these shores (Paine, 1974; 1976; Chilton and Bull, 1984) The role of crab predators in maintaining or structuring soft bottom communities, however, is still uncertain.

As a preliminary to understanding the mechanisms controlling structure and function in shallow water ecosystems, it is necessary to relate directly feeding activity of the predator and food availability. Changes in food availability may alter predator behaviour or seasonal activity of both predator and prey species. There are no previous studies providing both detailed information on the diet and the availability of prey species. Many studies on the diet of decapod and portunid crabs suggest, however, that they are opportunistic predators (Ropes, 1968; Elner, 1980; DuPreez, 1984; Haefner, 1985; Paul, 1981; Choy, 1986; Wear and Haddon, in press).

This study attempts to identify the food resources of the paddle crab and relate these to dietary composition of crabs collected seasonally from three locations in the Canterbury area.

The food resource included the infauna sand community and the surface community, including prey species present within epibenthic drift algae. Comparison of these samples with the dietary samples identifies any species able to avoid or escape predation. This study evaluates the role of the portunid crab Ovalipes catharus as an opportunistic feeder and discusses the likely effects of its foraging behaviour on the benthic community.

BANKS PENINSULA ENVIRONMENT

STUDY AREA

Banks Peninsula (Fig.12) is a volcanic promontory surrounded on three sides by the Pacific Ocean and on one side by the Canterbury Plains. The Peninsula is scarred with many bays including the first two study sites, Little Akaloa and Taylors Mistake. Little Akaloa, the most eastward sample site is 20 km seaward of Taylors Mistake and 25 km from Brighton Beach. Little Akaloa is an enclosed bay protected by the Peninsula on three sides, two of which stretch 4 km towards the open sea. Taylors Mistake, the first bay on the northern side of the Banks Peninsula is only partially protected from the open sea by 1 km of volcanic promontory. The third study site, Brighton Beach, is situated where the Canterbury Plains meet with the Peninsula and is typical of an east coast sandy beach, fully exposed to the Pacifics north-east seas. Extensive studies have been carried out on the hydrology, bathometry and sediments of the Brighton area.

The shore drops relatively steeply to approximately 12 m (Brown, 1976). Beyond this, the bottom slopes gently offshore with gradients of 1 in 3000. All Brighton Beach and Taylors Mistake samples were taken approximately 2 km offshore at a depth of 40 m. Little Akaloa samples were taken closer to shore at depths of 2-10 m.

The Canterbury Current flows northward around Banks Peninsula at a rate of 2 knots, creating an anticlockwise eddy (Brodie, 1960). This, when combined with large shoaling swells

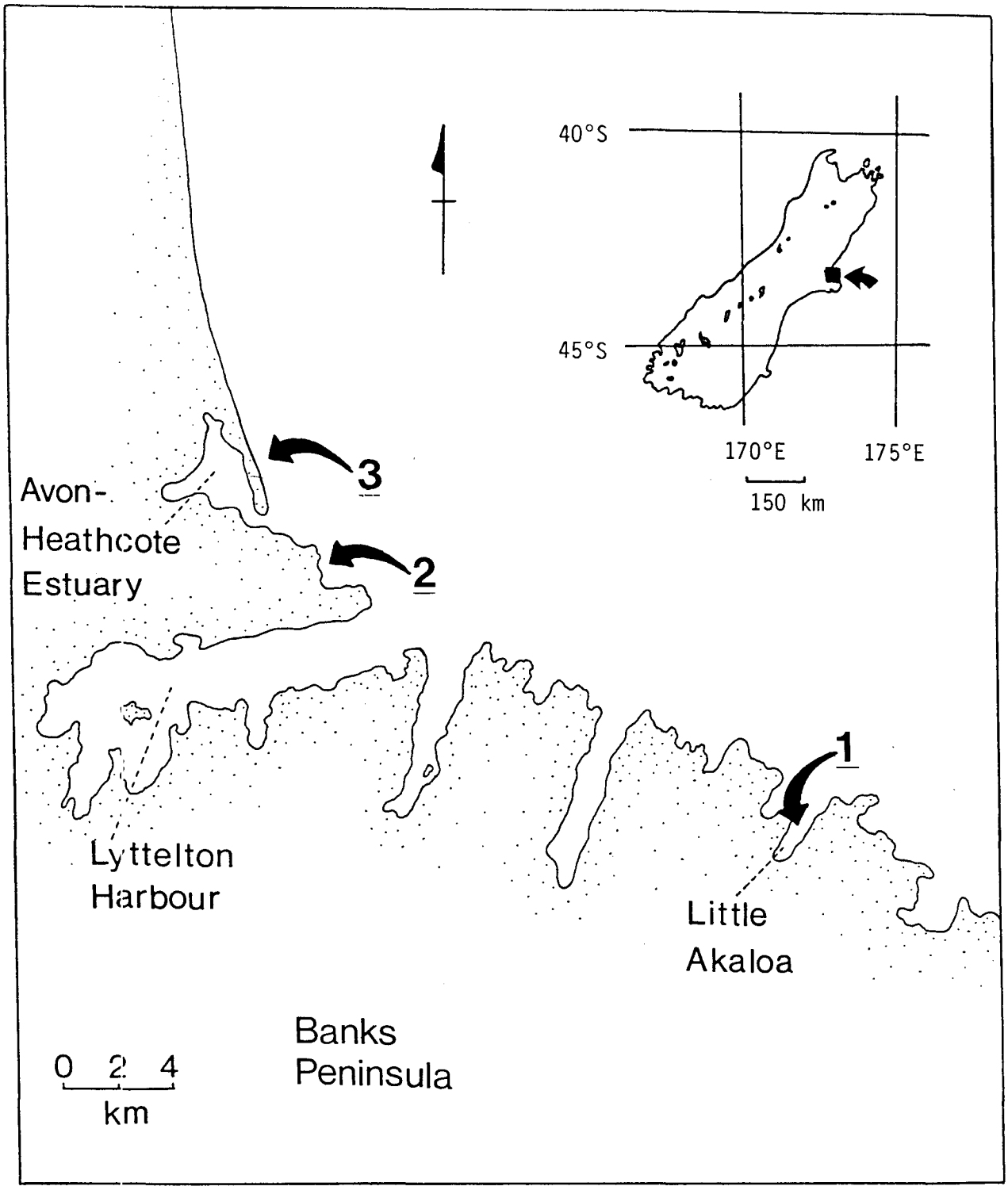


Fig 12. Northern side of Banks Peninsula; arrows indicate O. catharus sample sites: 1) Little Akaloa; 2) Taylors Mistake and; 3) Brighton Beach.

creates a significant drift, depositing various grades of sediments around the Peninsula.

SEDIMENTS

Benthic faunal studies have suggested a direct relationship between sediment type and animal distribution (Grange, 1977; Rhoads, 1974). It was therefore necessary to undertake a sediment analysis for samples from Little Akaloa in conjunction with benthic faunal samples. In the Brighton area, the sediment composition is known (Campbell, 1974) and a preliminary study on the benthic infauna was done by Knox et. al (1978).

Methods

The benthos at two Little Akaloa stations were sampled using coffee can samplers (see methods section under benthic survey for details) and a subsample (dry weight approximately 200 g) removed. Particle size analysis was carried out using a sediment shaker. Sediment values for the Brighton Beach and Taylors Mistake sites, were obtained from Campbell (1974) and Knox et al. (1978).

Results and Discussion

Table 7 presents the percent particle size composition by weight of the sediments using Wentworth size classes. The predominant sediment fraction present at the more exposed study sites, (Brighton Beach and Taylors Mistake) is very fine sand (particle size 0.0625-0.125 mm diameter). Silts and clays predominated at Little Akaloa, forming 70.4%. The high

Size Class (mm)	Sediment Type	Brighton Beach	Taylors Mistake	Little Akaloa
<0.0625	clay/silt	1.6%	21.0%	70.4%
0.0625–0.125	fine sand	48.4%	76.0%	27.7%
0.125 –1.0	coarse–fine sand	41.0%	2.5%	1.9%

Table 7. Percent particle size composition of the sediment at each study site (Wentworth size classes)

proportion of silts and clays at Little Akaloa is probably due to the enclosed and sheltered situation. Exposure to high wave energy and strong shore currents at Brighton Beach and Taylors Mistake carry silts and clays along, leaving the larger, heavier particles to settle out.

These results suggest that Little Akaloa sediments were most similar to those recorded near the mouth of the silt depositing Waimakariri River (Campbell, 1974). Knox et al. (1978) suggested that these sediments extend south and it seems most likely that they build up in the sheltered bays like Little Akaloa, lining the northern side of the peninsula.

TEMPERATURE

Materials and Methods

Temperatures for the first day in each month from April 1985 to April 1986 were obtained from New Zealand Meteorological Service satellite pictures. These were compared with temperatures taken by hand at each sample site during 26 September and 12 October, 1985.

Results and Discussion

Satellite derived temperatures are plotted in figure 13. Highest temperatures were recorded in late summer (17°C) and lowest temperatures in late winter, early spring (10°C). Comparison of satellite and thermometer readings show a discrepancy of approximately 2°C. This is posssibly due to the

difference in temperature between inshore shallow warmer waters recorded by hand and the deeper offshore waters recorded by satellite. Thermometer measurements taken by hand at the three sample sites measured within 0.2°C.

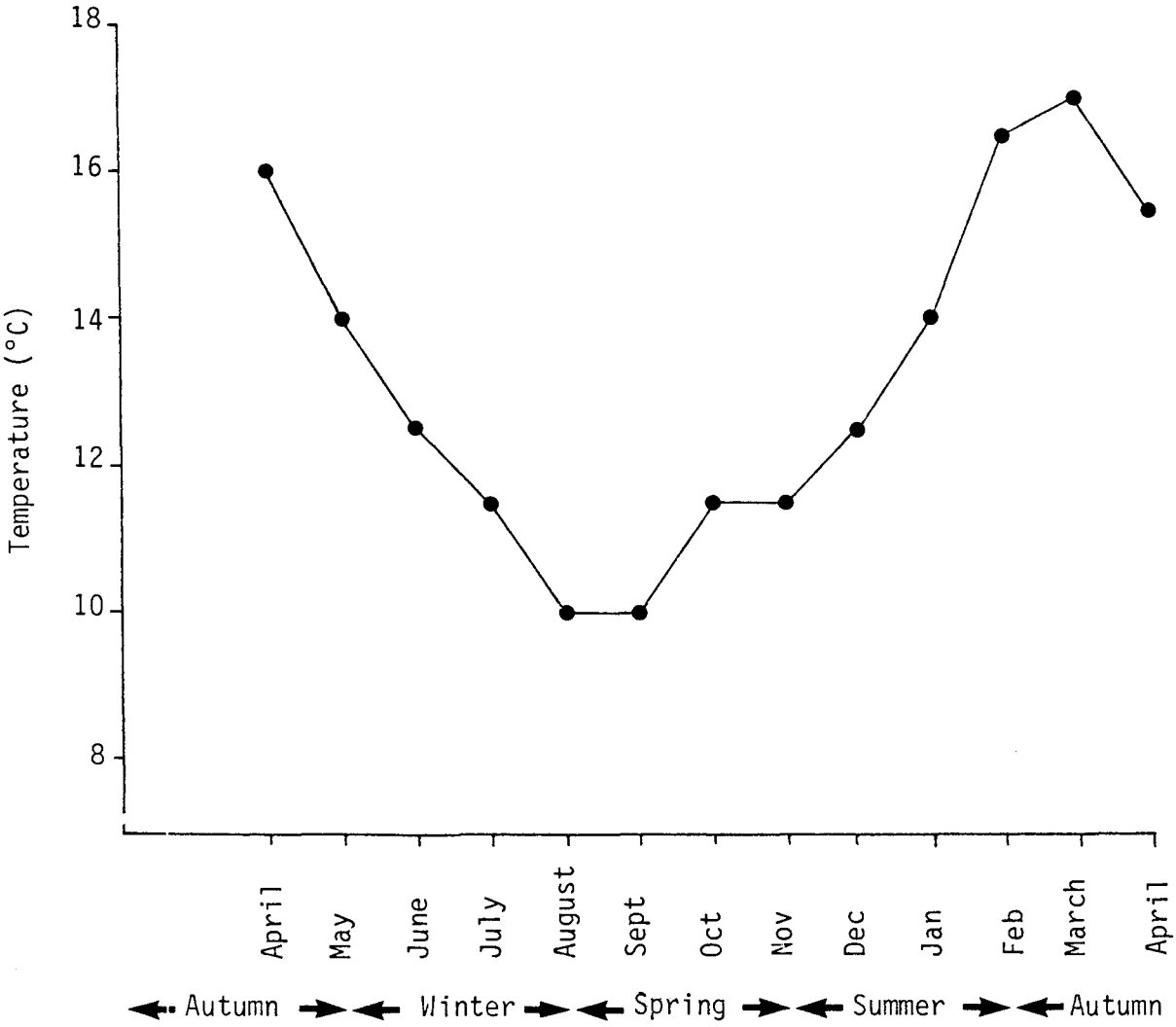


Fig 13. Canterbury coastal sea temperatures for 1985 - 86.

BENTHIC AND EPIBENTHIC FAUNA

INTRODUCTION

Within New Zealand there are very few quantitative studies providing information about the benthos in shallow sub-tidal habitats. Knox and Fenwick (1978) and Knox et al., (1978) suggested that subtidal habitats less than 30 m are composed of invertebrate faunas dominated by molluscs, crustaceans and polychaetes. Local reports (Knox et al., 1978) support these findings. However, community structure can best be related directly to the presence or abundance of paddle crabs.

During trawling for paddle crabs, it was noted that occasionally large quantities of drift algae were present in the habitat. This algae contained epifaunal macroinvertebrates, mainly crustacea. The presence of such items in the diet of paddle crabs confirmed the importance of drift algae as a food resource. Algae are often detached by storms, and can be washed ashore or sink to the sea bed (Bedford and Moore, 1984). Once dead, the mechanisms protecting the young frond tissue no longer function (Tenore and Rice, 1980) and bacteria and their associated macroconsumers flourish, providing a rich source of food.

Benthic macroinvertebrates were sampled seasonally from three sites to determine the community composition and seasonal variation in dominant species. These results provide information on the seasonal availability of prey to O. catharus and evaluate the role of drift algae in supplying additional food input into the environment.

MATERIALS AND METHODS

Infaunal Benthic Collections

Infaunal benthic macroinvertebrates were collected in sediment samples from two 10 m areas at Little Akaloa. Benthic samples were taken on SCUBA with 0.0125 m coffee can samplers, fitted at one end with 0.5 mm copper mesh. Five replicates were taken at each site to depths of 187 mm at three monthly intervals, from June 1985 to March 1986 inclusive. Samples were returned to the laboratory where they were sorted through a 0.5 mm sieve and the invertebrates identified and counted. Data from replicate samples (Appendix 2) were combined and composition was expressed as percentage abundance of the total number of animals counted.

In addition to describing the benthos taken in samples, community structure indicies were calculated to facilitate comparisons with the benthos from other sites and seasons. The Shannon-Weaver index was used as it is the most commonly used measure of species diversity (Peet, 1974) when the sample is best descibed by an average diversity (Pielou, 1966). This measure of diversity has the added advantage of being relatively sample-size independent. It is defined as:

$$H' = - \sum p_i \log_e p_i$$

where p_i is the proportion of individuals belonging to the ith species. Species diversity has a species richness component and an evenness component. Margalefs' (1958) measure of species

richness was used:

$$SR = (S-1) / (\log_e N)$$

where S is the number of species and N is the number of individuals. Evenness was calculated as:

$$J = H' / H'_{max}$$

where H'_{max} is log S.

Fenwick (1984) working in shelly sand benthos, recorded a critical collection depth for amphipods at approximately 40 mm. Similarly, Oliver (1980) collected 85.2% of all crustaceans above this level. Sampling to depths of 187 mm should therefore, capture the majority of the crustacean infauna. However, very deep dwelling molluscs such as the coot clam, Panopea zelandica (Powell, 1977; Powell, 1979) burrowing to a depth of 396 mm, would be missed by present sampling techniques. Although no quantitative measurement was possible for deeper burrowing animals, their burrows were physically excavated and their presence noted. The presence of very mobile animals such as Ovalipes catharus, which is able to avoid the benthic sampler, was also noted.

Epibenthic Faunal Collections

Epifaunal macroinvertebrates and vertebrates associated with the decaying drift algae were collected by trawling from Brighton

Beach, Taylors Mistake and Little Akaloa. Five replicates, each weighing approximately 150-200 g were collected and placed in plastic bags containing 10% formalin. Following transportation to the laboratory, samples were sorted, separated, identified counted, and related to wet weight of algae collected. The trawling method, although maintaining consistancy over all samples, was primarily designed to catch crabs. Consequently, some smaller invertebrates were able to escape through the large mesh. Algae building up in the net, however, provided a physical barrier and allowed collection of representative smaller species.

RESULTS

Benthic Faunas

Fifty-six species of macroinvertebrates were recognised from benthic samples (Table 8). Polychaeta were represented by the most species throughout the year (24), followed by Mollusca (9) and Amphipoda (8). Within the Crustacea there were 3 Cumacea species, 2 Ostracoda, 1 Leptostraca and a few representatives of the Decapoda, Isopoda and Tanaidacea. Archelia dohrni a Pycnogonida, and two species of Echinodermata were also recorded (Table 3).

No significant difference was recorded between sites. Therefore, all replicates were combined and represented as percentage abundance (Table 9). Seasonal data were also combined into an all samples group, giving a total of 35 benthic samples. Polychaetes were consistently the most abundant infaunal group with values as high as 85.2%, recorded in winter. Capitellidae, Orbina papillosa and Scolopos sp. were present all year round and

Table 8. List of benthic organisms collected from Little Akaloa, cllected 1985-1986.

PHYLUM : MOLLUSCA

Class Gastropoda

Amalda australis (Sowerby, 1830)

Class Bivalvia

Divaricella huttoniana (Vanatta, 1901)
Dosinia sp. Scopoli, 1777
Gari strangeri (Gray, 1843)
Mactra ovata (Gray, 1843)
Myadora striata (Quoy & Gaimard, 1835)
Nucula hartivigiana Pfeiffer, 1864
Panopea zelandica (Quoy & Gaimard, 1835)
Tellina (Macomona) liliana Iredale, 1915
Tellina (Tellina) sp. Mörch, 1853

PHYLUM : ANNELIDA

Class Polychaeta

Aglaophamus sp. Kinberg, 1866
Armandia sp. Filippi, 1861
Capitellidae sp. Grube, 1862
Cirriformia sp. Hartman, 1936
Cirratulidae sp. Carus, 1863
Cossura sp. (Webster & Benedict, 1887)
Glycera americana Leidy, 1855
Heteromastides filiformis(Claparede,1864)
Lepidastheniella sp. Malmgren, 1867
Lumbrinereis sp. Blainville, 1828
Maldanidae sp. Malmgren, 1867
Magelondidae sp. Cunningham & Ramage, 1888
Nereidae sp. Johnston, 1845
Opheliidae sp. Malmgren, 1867
Ophelina sp. Salvigny, 1818
Orbinidae sp. Hartman, 1942
Orbina papillosa (Ehlers, 1907)
Paraonidae sp. Cerruti, 1909
Pectinaria sp. Lamarck
Polydora sp. Bosc, 1802
Sabellidae sp. Malmgren, 1867
Scolopos sp. Blainville, 1828
Sigalionidae sp. Malmgren, 1867
Sphaerodoridae sp. Malmgren, 1867

PHYLUM : ARTHROPODA

Class Crustacea

Subclass Ostracoda

Ostracoda sp.#1
Ostracoda sp.#2

Subclass Malacostraca

Leptostraca sp.

Order Cumacea
Diastylidae sp.#1
Diastylidae sp.#2
Diastylidae sp.#3
Order Tanaidae
Tanaidae sp.
Order Amphipoda
Amphipod sp#1
Amphipod sp#2
Atylus taupo Chilton, 1923
Liljeborgia hansoni Hurley, 1954
Lysianassidae sp.
Oedediceratidae sp.
Photis nigrocula Lowry, 1979
Phoxocephalid sp#1
Phoxocephalid sp#2
Order Isopoda
Anthuridae sp.
Glycerida sp.
Janiridae sp.
Order Decapoda
Helice crassa Dana, 1851

Class Pycnogonida
Achelia dohrni (Thomson, 1884)

Class Ophiuroidea
Amphiura aster Farquhar, 1901

Class Echinoidea
Asterninia regularis Verril
Fellaster zelandiae (Gray, 1855)

Food Type	June n=5	Sept n=10	December n=10	March n=10	All Months n=35
Gastropoda	2.3		0.5	0.6	
Bivalvia	0.5	3.1	5.1	5.5	2.1
Capitellidae	39.0	25.0	9.1	1.4	20.4
Malegelongidae	14.0	27.3	28.3	13.7	17.2
Maldanidae	0.5	7.0	1.0	4.6	3.2
Orbina papillosa	3.7	5.5	2.0	14.6	7.3
Scolopus sp.	13.5	1.6	10.1	10.0	8.5
TOTAL POLYCHAETES	80.9	85.2	63.6	53.9	64.4
Cumacea	1.4	1.6			0.8
Ostracoda	2.3	2.3	3.0	2.3	2.4
TOTAL AMPHIPODA	11.2	8.6	17.1	31.5	18.3
Phoxocephalid spp.	1.9	6.3	12.1	15.5	10.7
Isopoda	2.8		4.0	0.9	1.8
Decapoda			2.0		0.3
Achelia dohrni	0.5				0.2
Tanaidacea				2.7	0.9
Ophiuroidea	0.5		1.0		0.6
TOTAL NUMBER	215	128	99	219	661
TOTAL NUMBER PER 0.0125 m	43.0	12.8	9.9	21.9	18.8

Table 9. Percentage abundances of benthic faunas collected from Little Akaloa, June 1985 to March 1986.

comprised the majority of polychaetes. Amphipoda represented 8.0-31.5%, followed by Bivalvia 0.5-5.5%.

Small sample variation for most species within each month, suggested that an adequate description of the benthos was obtained. Because of the notoriously patchy nature of this environment, the degree of continuity with adjacent areas is always under speculation.

Seasonal changes of benthic macroinvertebrates are well documented (Boesch, 1973; Kikuchi and Tanaka, 1978; Witling, 1975; Whitlatch, 1977). Figure 14 describes the mean number of polychaetes, crustaceans and molluscs recorded from Little Akaloa. Polychaetes and crustaceans reached highest densities in late autumn to early winter. Crustaceans declined to a minimum in early spring, while polychaete numbers were lowest in early summer. High polychaete numbers in early winter (2480 per m^2) were due to heavy concentrations of Capitellids in samples. Percentage abundance of molluscs remained relatively constant over the entire sampling period, with the bivalve Mactra ovata and the gastropod Amalda australis present in most samples. Other mollusc species including the clam Nucula hartvigiana occurred in samples sporadically and in low numbers.

Indicies of community structure are useful in further describing the benthic fauna, and Table 10 lists for each season the species diversity (H') and its components, species richness (SR) and evenness (J').

Species diversity varied considerably seasonally. Highest diversity was recorded for autumn (4.198) and early winter (2.143) with lowest values in spring (1.586) and summer (1.779).

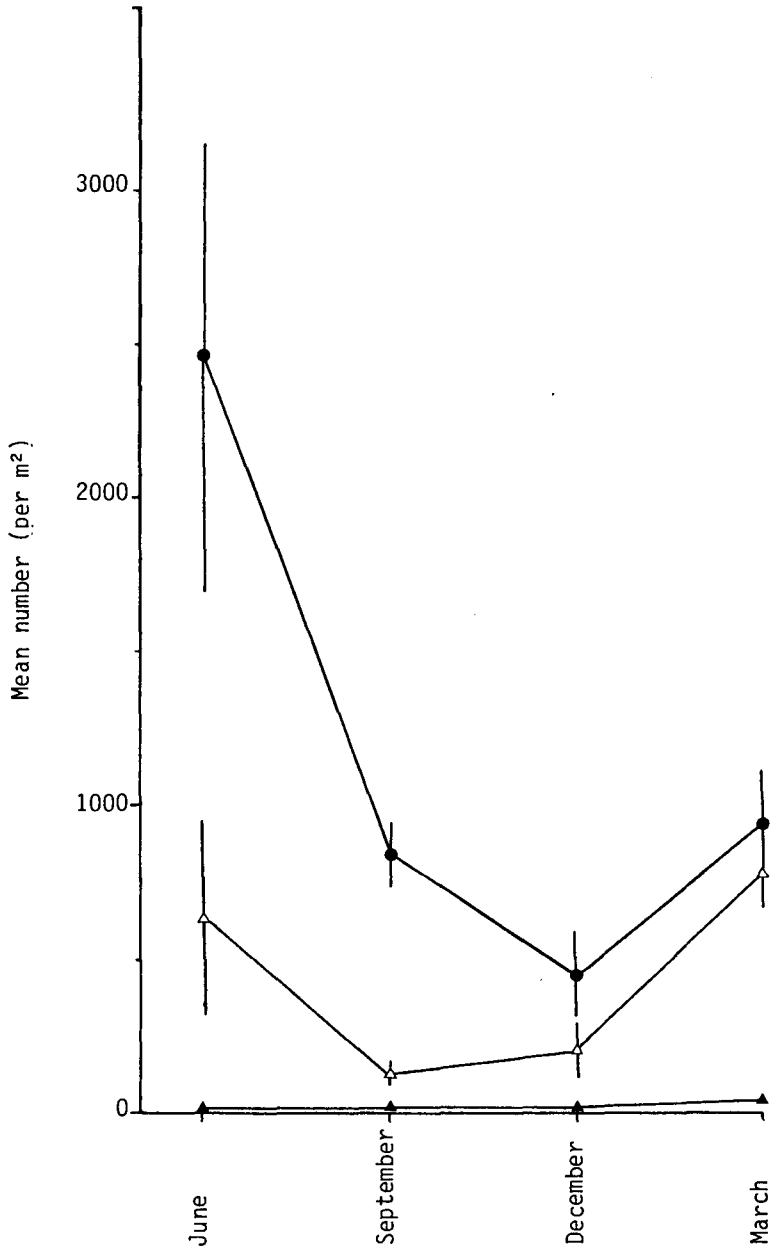


Fig 14. Mean number of benthic organisms (per m²) collected seasonally at Little Akaloa, 1985-86. Closed circles represent Polychaeta, open triangles Crustacea and closed triangles Mollusca.

Month and Season	n	S	H′	SR	J′
June (Winter) *	215	26	2.143	4.655	0.6577
Sept (Spring)	130	23	1.586	4.520	0.5058
Dec (Summer)	100	28	1.779	5.865	0.5339
March (Autumn)	220	35	4.198	6.304	1.1808

Table 10. Number of individuals (n), number of species (S), species diversity (H′) species richness (SR) and evenness (J′) for each season (10 samples covering a total of 0.125 m^2, * 5 samples covering 0.0625 m^2)

Algae	Origin	Brighton Beach	Taylors Mistake	Little Akaloa
Chlorophyceae				
Enteromorpha sp.	S,R			*
Ulva sp.	S,M	*	*	*
Phaeophyceae				
Carpophyllum sp.	S,R	*		*
Cystophora sp.	S,R	*		*
Macrocystis pyrifera	S,R	*	*	*
Sytouthamnus sp.	M,R		*	
Rhodophyceae				
Ballia callitricha	E,R		*	
Gigartina sp.	E,R	*	*	*
Plocamium sp.	E,R	*	*	*
Rhodymenia sp.	E,R	*	*	
Terrestrial		*	*	*

Table 11. Drift algae representations at the three sample locations. Type of shore exposure where living algae originated are given: S = sheltered shore origin, M = moderate, E = exposed while R = rocky shore and Z = soft bottom

Highest water temperatures in autumn and early winter (Fig.13), corresponded with highest diversity indicies (Table 10). Similarly, lower species diversities were recorded in the cooler months. Species richness and evenness values showed similar patterns.

Epibenthic Faunas

A total of eleven species of drift algae were collected, eight from Little Akaloa and seven species from Brighton Beach and Taylors Mistake (Table 11). Most of the species are characteristic of rocky shores. Macrocystis pyrifera, Enteromorpha sp. and Ulva probably originating from sheltered shores and Plocamium sp. and Ballia callitricha from more exposed shores. All the species were commonly found on the northern side of Banks Peninsula and provide a rich source of drift algae following large storms.

Fifty-four species of animals were recognised from drift algae samples (Table 12, Appendix 2). Little Akaloa was represented by 45 species followed by Brighton Beach with 30 and Taylors Mistake with 24 species. Eighteen species were found at all three stations on Banks Peninsula, of these five were decapods. Decapoda were represented by the most species (11), Mollusca (8), Polychaeta (7) and Amphipoda (6). Also present were representatives of the Turbellaria, Nematoda, Ostracoda, Mysidacea, Echinodermata and Teleostei (Table 12).

Percentage abundances of the epibenthic fauna derived from combined replicates are represented in Table 13 and 14. Amphipoda were the most important group at all sites and seasons.

Table 12. List of epibenthic organisms collected from Little Akaloa, Brighton Beach and Taylors Mistake, collected 1985-1986.

PHYLUM : COELENTERATA
* ! Hydrozoid sp.

PHYLUM : PLATYHELMINTHES
* Order Turbellaria

PHYLUM : NEMATODA
*

PHYLUM : MOLLUSCA

Class Gastropoda
*+ Amalda australis (Sowerby, 1830)
! Melagraphia aethops (Gmelin,1791)
* Patellidae sp.
* Pleurobranchiidae sp.
* Xymene sp. Iredale, 1915

Class Polyplacophora
* Chitonidae sp.

Class Bivalvia
+ ! Perna canaliculus (Gmelin, 1791)

Class Cephalopoda
* Sepioloidea pacifica (T.W.Kirk, 1882)

PHYLUM : ANNELIDA

Class Polychaeta
* Cirratulidae sp. Carus, 1863
* Eunicidae sp. Salvigny, 1818
* Lumbrinereis sp. Blainville, 1828
*+! Nereidae sp. Johnston, 1845
* Orbina papillosa (Ehlers, 1907)
*+! Perinereis sp. Kinberg, 1866
\+ Sigalionidae sp. Malmgren, 1867

PHYLUM : ARTHROPODA

Class Crustacea
Subclass Ostracoda
* Ostracoda sp.
Order Mysidacea
*+! Mysid sp.
Order Cumacea
* Diastylidae sp.#1
* Diastylidae sp.#2
* Diastylidae sp.#3

Order Amphipoda
*+! Allorchestes sp.
*+! Atylus taupo
*+! Amphipod sp.#1
*+! Amphipod sp.#2
*+! Amphipod sp.#3
*+ Phoxocephalidae sp.
Suborder Cymamidea
* Caprellidea sp.
Order Isopoda
*+ Aegidae sp.
* Anthuriidae sp.
*+! Zenobiana tubicola (Thompson)
Order Decapoda
*+ Cancer novaezelandiae (Jacquinot, 1837)
*+! Crangon sp.
* Hemigrapsus crenulatus (Milne Edwards, 1837)
* Halicarcinus cookii (Filhol, 1885)
*+ Halicarcinus innominatus Richardson, 1949
* Halicarcinus pubescens
*+! Hymenosoma depressum Jacquinot, 1853
*+! Megalopa
*+! Ovalipes catharus (White, 1843)
+! Peneidae sp.
*+! Petrolisthes elongatus (Milne Edwards, 1837)

Class Pycnogonida
*+ Achelia dohrni (Thomson, 1884)

PHYLUM : ECHINODERMATA

Class Echinoidea
*+! Asterninia regularis Verril
*+! Fellaster zelandiae (Gray, 1801)

Class Ophiuroidea
* Amphiura aster Farquhar, 1901

PHYLUM : TELEOSTEI
+ Aldrichetta forsteri(Cuvier & Valencienness)
*+! Pseudophycis bachus(Bloch & Schneider, 1801)
+ Rajidae sp.
*+! Rhombosolea retiaria Hutton, 1874
+! Sphoeroides richei (Anon, 1798)

Records from : * Little Akaloa; + Brighton Beach; ! Taylors Mistake

Food Type	June n=5	Sept n=10	December n=5	March n=5	All Months n=25
Turbellaria	0.3				*
Nematoda	1.4				*
Gastropoda	0.3		1.2		0.5
Chitonidae			0.1		*
Perna canaliculus			0.6	2.7	0.8
TOTAL POLYCHAETES	2.1		0.6	2.7	0.8
Cumacea	0.3				*
Ostracoda	1.6				*
Mysidacea	4.5		0.1		0.8
Allorchestes sp.	26.4	49.7	71.2	66.1	56.7
Atylus taupo	4.5	35.5	9.9	2.9	17.1
TOTAL AMPHIPODA	83.8	95.9	88.7	77.1	90.4
Zenobiana tubicola	1.2	*	0.6	0.7	0.6
TOTAL ISOPODA	2.1	*	0.6	1.4	0.8
Decapoda	3.4	1.5	4.5	10.0	3.3
Achelia dohrni	0.9	1.5	3.5	3.5	2.4
Echinoidea				3.5	0.3
Ophiuroidea					
Teleostei			0.8	1.1	0.4
TOTAL NUMBER	646	647	646	121	2090
TOTAL NUMBER PER 0.0125 m	87.5	24.9	64.3	13.9	43.5

Table 13. Percentage abundances of epibenthic organisms collected from Little Akaloa, June 1985 to March 1986. An * indicates that the food type was present but formed less than 0.1% of the total for that sample

Food Type	October n=3	March n=8	All Months n=11
Turbellaria	(5.0)		0.1
Nematoda			
Gastropoda		0.1(1.2)	0.2
Chitonidae			
Perna canaliculus	(5.0)	46.2	19.2
TOTAL POLYCHAETES	0.3(5.0)	0.8(4.8)	0.9
Cumacea			
Mysidacea	17.6(2.8)	0.3(0.9)	8.6
Ostracoda			
Allorchestes sp.	64.0(56.7)	39.5(52.4)	53.4
Atylus taupo	10.7(5.0)		5.2
TOTAL AMPHIPODA	75.7(64.5)	40.0(65.7)	59.8
Zenobiana tubicola	4.6(5.0)	6.5	5.1
TOTAL ISOPODA		7.1(1.6)	5.4
Decapoda	1.6(12.8)	5.7(26.0)	5.5
Achelia dohrni	0.3		0.1
Echinoidea			
Ophiuroidea		0.2	*
Teleostei		0.3	0.1
TOTAL NUMBER	324(40)	493(76)	933
TOTAL NUMBER PER 0.0125 m	224(28.2)	78.3(25.3)	84.8

Taylors Mistake figures represented in brackets

Table 14. Percentage abundances of epibenthic organisms collected from Brighton Beach and Taylors Mistake, October 1985 to March 1986.

Amphipods comprised 77.1-95.9% at Little Akaloa (Fig.15), 40-75.7% at Brighton Beach and 64.5-65.7% at Taylors Mistake. Atylus taupo and Allorchestes sp. were present at all sites and constituted the majority of amphipods. The green lipped mussel, Perna canaliculus was patchily distributed. It was found in large numbers (362 per 100 g wet algae) on hydroid colonies in one sample at Brighton Beach and in one sample at Taylors Mistake. Decapods were collected at all sites and formed the second most abundant group (1.6-26%). Five species of hymenosomatids were often collected at all locations throughout the entire sampling period.

Results suggest that most animals associated with the epibenthic drift algae, (nos per 100 g) are seasonal. Densities and the degree of fluctuation differed at each locality. Epibenthic macrofauna at Little Akaloa reached maximum densities in late autumn and early summer. Peaks in animal numbers at Brighton Beach and Taylors Mistake occurred in spring and were followed by sharp declines in summer. This was followed in turn by an increase in invertebrate numbers in autumn. Algae abundance was highest in autumn following storms and northerly swells which detach living plants. Highest densities of animals were recorded from Brighton Beach, when algae catches were high requiring a winch to bring the trawl onboard. Two months later, no algae and few animals were collected in the trawls, supporting the positive association between invertebrate densities and the abundance of drift algae.

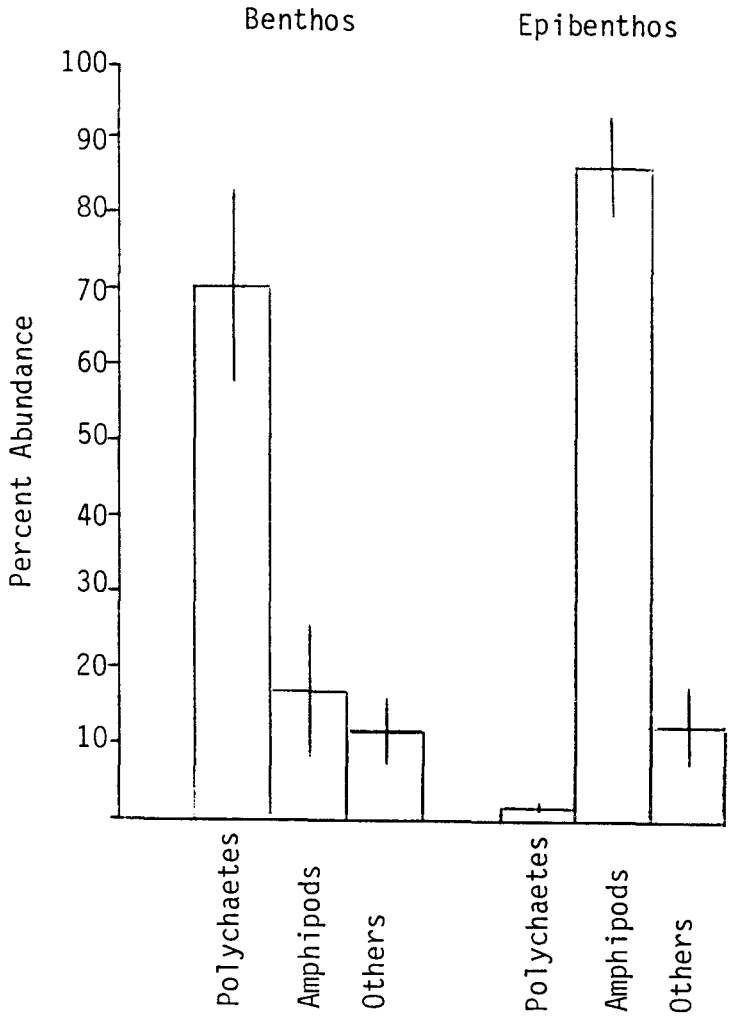


Fig 15. Percent abundance of 3 major animal categories found in the benthos and epibenthos at Little Akaloa, collected June 1985 to March 1986. Error bars represent 95% confidence limits.

DISCUSSION

Benthic Infauna

The benthos of subtidal habitats in the Canterbury area is varied both with location and season. Communities were dominated by relatively few species which was consistant with trends seen in studies elsewhere (Boesch,1973; Watling, 1974; Kikuchi and Tanaka, 1978; Fenwick, 1984). Seasonal changes in faunal assemblages were recorded at Litle Akaloa. These changes in faunal assemblages may represent successional changes. In soft bottom habitats seasonal recruitment and growth rates of dominant animals results in seasonal compositional changes (Kikuchi and Tanaka, 1978). Polychaetes such as Orbina papillosa, Scolopos sp. and Capitellidae were responsible for changes in community at Little Akaloa. Population cycles and fluctuations have been recorded previously for the polychaetes Capitella capitella (Watling, 1974) and Boesch (1973) suggested seasonal patterns in benthic communities were in response to recruitment and depletion of populations of seasonally spawning species. At Little Akaloa, high species diversity values in March suggested that the majority of benthic organisms have reproductive peaks in autumn and early winter. Increased species diversity in spring probably coincided with settlement of many crustaceans and bivalves.

The fauna from the sheltered mud-silt substrata of Little Akaloa contrasted with the fauna collected from the exposed fine sand of Spencerville (Knox et.al., 1978). Species associated with the high energy surf zone of Spencerville, including the bivalve Mactra discors, the amphipod Patuki breviuropodus and the shrimp Callianassa filholi were missing from Little Akaloa collections.

Of the 55 species recorded at Little Akaloa only 43.6% were also found at Spencerville. Boesch (1973), found that substrata was the overwhelming factor responsible for the spatial patterns and species distribution in the Hampton area Virginia. Similar conclusions were made by Knox et al., (1978) and Knox and Fenwick (1978) at Spencerville and Hawke Bay. Sand substratum, conceivably presents greater interstitial living space to the infauna than mud bottoms, where infauna are limited to the looser packed sediments near the surface. Thus, the greater spatial heterogeneity (Pianka, 1966; Sanders, 1968) allowed greater species diversity on sand bottoms than on mud.

Indicies of benthic community structure calculated for Spencerville (Knox et al., 1978) are considerably higher than those recorded at Little Akaloa. Little Akaloa species diversity (H') in September-October was 1.6 while at Spencerville was 2.7-3.1. Species richness value for Little Akaloa was 4.5 compared with 5.7-7.9 at Spencerville. Evenness showed similar trends: 0.51 at Little Akaloa compared with 0.462-0.929 at Spencerville. These results suggest a greater community complexity at the exposed sandy bottom situation at Spencerville. Knox et al.(1978) and Knox and Fenwick (1978) compared the sediments of Pegasus Bay with those of Hawke Bay and concluded that differences in community structure could be accounted for by sediment type. The predominance of fine sand at Pegasus Bay and silt-clay at Little Akaloa is the most plausible reason for the observed differences in community structure in this present study.

Epibenthic Fauna

Large storms in winter and rolling northerly swells in summer deposit large quantities of algae on the sediment surface around Banks Peninsula. This drift algae is colonised by a wide range of organisms, influenced largely by the amount and type of algae (Bedford and Moore, 1984). Peak densities of these organisms soon decline as the algae decompose. The rate of algae decomposition is rapid as the distal fronds are already decaying when the plant is detached (Johnston et al., 1977). The decaying action of microinvertebrates, however, is slowed down by the presence of macroinvertebrates which consume large numbers of these bacteria and unicellular organisms (Bedford and Moore, 1984). The rate of decomposition is therefore, also a factor of macroinvertebrate abundance and inturn the level of predation.

The macrofauna associated with decaying drift algae in the Banks Peninsula area was temporary in nature. Population densities of macrofauna increased with the density of algae and numbers decreased following the disappearance of the plant material. Mean densities of 224 animals per 100 g wet algae were recorded on Brighton Beach during October, while two months later, no algae was found and only a few animals recorded. Animal density climbed to 78.3 per 100 g of algae following the deposition of algae in summer storms.. Similar trends were recorded at Little Akaloa with peaks in June (87.5) and December (64.3), both followed by reduced densities in August (24.9) and March (13.9). Results suggest that rapid increase of macroinvertebrate numbers associated with drift algae, may be due

to their close association with living algae prior to dislodgement.

Considerable changes in species diversity and seasonal patterns in community structure were found in both the benthos and epibenthos. However, the factors responsible for these changes can only be discussed cautiously.

From the densities of paddle crabs found in the Canterbury region, it seems unlikely that food resources are limiting. The food resource includes both permanent members of the benthos and temporary inhabitants of the surface layer. This study has identified the role of fauna associated with epibenthic algae as a food source, however, other prey may also be available. O. catharus, may also feed on larger planktonic organisms, euphausiids, shrimps and juvenile fish. During settlement periods of bivalves additional, easily available prey becomes locally abundant. Predation by O. catharus may be important in the regulation of such subtidal communities.

NATURAL FOOD OF THE PADDLE CRAB

INTRODUCTION

Natural diet studies on crabs are usually based on stomach contents. Positive identification is often difficult due to food shredding by the mouth parts and further mastication by the gastric mill in the foregut. Another feature important to consider is the passage time of food within the foregut. Prolonged foregut passage time may result in the analysis of two or more feeding bouts making the investigation of diet composition in any one period suspect. For foregut analyses to accurately represent the composition of the diet, it is important to understand the masticatory processes and estimate foregut clearance and efficiency. For Ovalipes catharus, this information is outlined as a preliminary to the dietary studies.

Four main methods have been used to study the natural diet of crabs. Firstly, frequency occurrence, records the number of stomachs containing one or more individuals. This method was used for Carcinus maenas (Ropes, 1968; Elner, 1981), Cancer magister (Gotshall, 1977), Callinectes sapidus, C. toxotes (Paul, 1981), Portunis pelagicus (Williams, 1981; 1982), Paralithodes camtschatica (Jewett and Feder, 1982), Ovalipes stephensoni (Haefner, 1985) and Ovalipes catharus (Wear and Haddon, in press). Secondly, numerical occurrence, records the number of individuals in each food category for all stomachs with the total, expressed as a percentage of the total individuals in all food categories. Thirdly, volumetric composition, where the displacement of each food item is measured or estimated visually from the total stomach contents (Elner, 1981; Jewett and Feder,

1982). Finally, gravimetric composition, where the weight of prey types is determined wet or dry. This latter technique is impractical for crab diet studies as most of the organisms found in the foregut have been crushed and are inseparable from the other stomach contents.

The Index of Relative Importance (IRI)(Pinkas et al., 1971), incorporates frequency, numerical and volumetric measures of dietary importance and was used in this study to investigate the feeding habits of the paddle crab Ovalipes catharus, from three Canterbury locations on a seasonal basis. Until recently (Pinkas et.al., 1971; Stevens et al., 1982; Mitchell, 1984) IRI has not been widely used. Hyslop (1980) attributed this to the limitation of IRI as an index to compare between studies. The use of IRI here, aims at a more accurate measure of food importance, while increasing the number of studies available for dietary assessment comparisons. The compound nature of this method allows tests to be made on any or all of its components, an advantage over a single value of diet composition

Compound indicies of dietary importance minimize problems inherent with each part of the equation. Problems associated with frequency and numerical occurrence arise from biases in favour of recognisable hard parts (eg. carapace, shell, bone) and small items (eg. hydroids, ostracods, cumaceans) which may contribute little towards food value. Percentage volume estimates are biased against items which digest rapidly, such as polychaetes (Kennedy, 1969). Regardless of which method is used, however, the important food items are always distinguished from rare or less important foods (Elner, 1981; Williams, 1981). To

reduce bias in dietary assessments, crab foreguts were collected from three locations on a seasonal basis as close as possible crab feeding periods. The time flesh and hard parts, items used to identify dietary importance remained in the crab foregut were also determined in laboratory experiments. These data on the natural diet of paddle crabs and information on food availability allowec crab feeding strategies to be determined and the impact of precation by crabs to be assessed.

FOREGUT STRUCTURE, FUNCTION AND FOOD PASSAGE TIME

Introduction

The rate of digestion exerts considerable influence on the state of food in the foregut and ultimately the accuracy of diet analyses (Hyslop, 1980). Factors found to influence digestion rates include the indigestable hard parts possessed by the food items (Williams, 1981), water temperature (Baldwin, 1957) and prey fat content (Elliott, 1972). Differential digestion rates could therefore, cause biases in favour of particular types of prey. This was investigated using foregut passage time experiments.

Food passage time experiments were designed to determine the period of time soft flesh remained in the foregut and how long hard parts were present before their regurgitation. Hill (1976) found hard parts in the diet of the crab Scylla serrata remained in the foregut for anything up to eight days. Similar results for O. catharus would significantly influence the accuracy of a dietary study.

Materials and Methods

Rates of foregut clearance for soft organic food and indigestable shell were determined for the paddle crab, Ovalipes catharus captured in trawls 1 km offshore at Brighton Beach, Canterbury. Individual (50-70 mm carapace width) crabs were starved for seven days before experimentation in a closed seawater system at 18°C 1°C. Foregut passage time of soft organic food and clearance rate of shell was determined using six freshly crushed blue mussels, Mytilus edulis aoteanus (15-20 mm), fed to crabs over a 15 minute period. Individual crabs which did not consume all five mussels were rejected. Shell debris was removed from the aquaria floors and stomach contents examined at intervals of 0, 1, 2, 3, 6, 9, 12 and 24 h. Soft organic matter and shell present in the foregut was separated dried and weighed. Percentage weight of food ingested from that presented to crabs was calculated using total shell and flesh weights. These were derived using the equations:

ln mussel flesh weight = 2.78 ln mussel length (5-35 mm)-10.99
$r = .99$, $n = 20$.

ln mussel shell weight = 4.34 ln mussel length (15-25 mm)-13.57
$r = .98$, $n = 12$.

RESULTS AND DISCUSSION

Foregut Structure and Function

The foregut of O. catharus (Fig.16) consists of two regions. Firstly, an anterior section composed of a large membranous cardiac-stomach into which the oesophagus opens. Secondly, a posterior region composed of a smaller pyloric stomach containing the gastric mill. The pyloric stomach opens into the hindgut and digestive glands. Food, partially shredded by the dimorphic chelipeds (Davidson and Marsden, in press) and mouthparts, enters the cardiac region of the oesophagus where it is mixed with digestive juices from the digestive gland (Younge, 1924). This mixture is ground into a pulp of particles and liquids by the gastric mill and sorted according to the particle size (Schaefner, 1970).

The gastric mill (Fig.16), is a complex set of ossicles, teeth and spines, controlled by extrinsic muscles. These act to grind the food (Caine, 1974) and push it towards the pyloric stomach where it is sorted and passed to either the filters, hindgut or digestive gland depending on the particular size (Schaefner, 1970)

The structure of the crab gastric mill can be related functionally to the size and type of food arriving (Skilleter and Anderson, 1986). The dorsal tooth of the gastric mill in O. catharus is a hardened concave structure which probably cuts food along its edge and grinds it in the mortar shaped part of the tooth. The lateral teeth carry a row of equally hardened knobs, which diminish in size posteriorly forming a serrated cutting

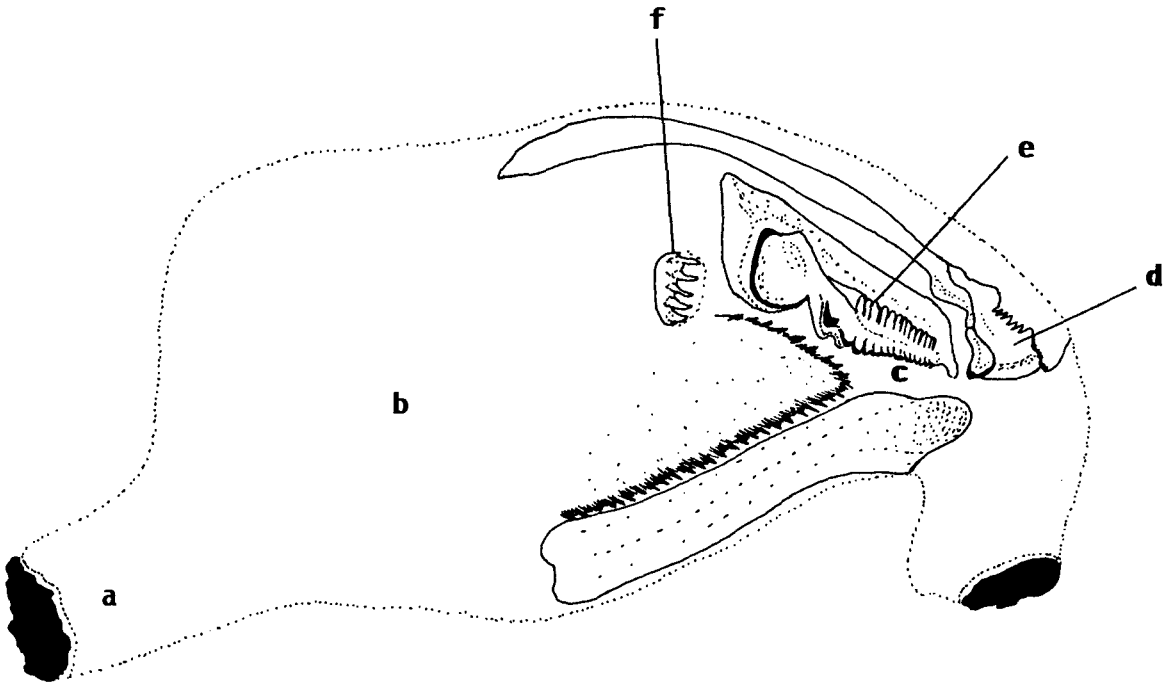


Fig 16. Lateral view of the foregut of Ovalipes catharus: a) Oesophagus; b) cardiac stomach; c) phyloric stomach; d) dorsal tooth of gastric mill; e) lateral teeth; f) lateral accessory teeth.

edge and grinding surface. There are a large number of stout setae and lateral accessory teeth (Fig.16) which probably assist in preventing food escaping anteriorly from the gastric mill. The structure of the gastric mill suggests that it would cope with coarse material requiring cutting, grinding and mascerating prior to digestion.

Foregut Passage Time

The mean percent mussel flesh remaining in the foregut of O.catharus 15 minutes after consumption was 23%±7.36 (2 x standard error; n=5) of that presented (Fig.17). This represented an ingestion loss of flesh between 70-90 % which is greater than 27% loss reported by Hill (1976) and Dagg (1974). In Hills experiments using Scylla serrata crabs were fed on prawn's abdomers. Comparison of these results suggests that the nature of the food affects the ingestion efficiency of crabs. Paddle crabs had difficulty extracting all the flesh from the mussel shell and rejected the most difficult portions. Also the soft flesh of mussels lead to considerable fragmentation during manipulation resulting in greater tissue loss. These two features together with the more muscular nature of food presented to Scylla in Hills experiments, probably explains the greater ingestion loss.

In Ovalipes, the proportion of flesh ingested compared with that presented initially declined (Fig 18) to approximately 5-10% after 1-3 h ingestion (Fig.17). After 12 h, no discernable flesh remained in the foregut of Ovalipes catharus. Because of the rapid rate of foregut clearance in O. catharus, the presence of

organic material in the foregut of field collected crabs probably indicates a recent foraging bout.

Figure 17 shows that paddle crabs ingested only 6.3% ± 2.3 (2 x standard error, n=5) of the original shell presented. The amount of shell declined little over the next 8 hours, however, by 12 hours, only one crab out of five retained a trace of shell fragments (Fig.17,18). By 24 hours, no shell was present in the foregut (n = 12). Hill (1976) found that half of all S. serrata retained shell for up to 5-6 days. The author concluded, that gut analysis based upon hard parts in the foregut would be biased in favour of shelled animals. For O. catharus, rapid foregut clearance of soft tissue and shell fragments would not bias studies due to hard parts remaining in the foregut from previous days feeding. Foregut samples should provide an accurate indication of the diet up to 12 h previous to capture. The field collection of crabs within two hours of peak feeding time, minimizes the loss of rapidly disappearing items such as polychaetes.

In Ovalipes, the rapid loss of food from the foregut within 2-3 h was probably due to the grinding action of the gastric mill, partial digestion by enzymes, and the passage of food to the midgut and digestive gland. Hill (1976) suggested that the rapid clearance of organic material by S. serrata enabled crabs to fill the foregut more than once a night. For O. catharus, this process is enhanced by rapid clearance of inorganic material such as shell at the same rate flesh is cleared.

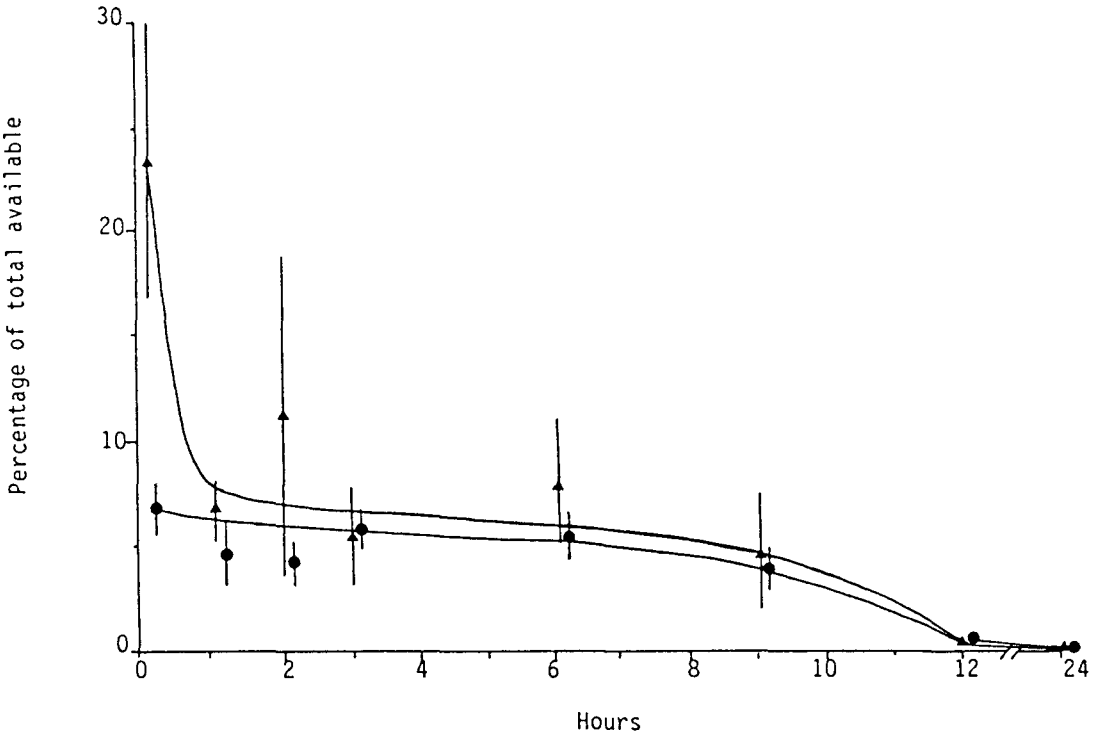


Fig 17. Percentage of total available flesh and shell remaining in the foregut of O. catharus relative to hours of digestion. Triangles represent shell (n=35) closed circles represents flesh (n=35). Error bars represent 95% confidence limits. Curves fitted by eye.

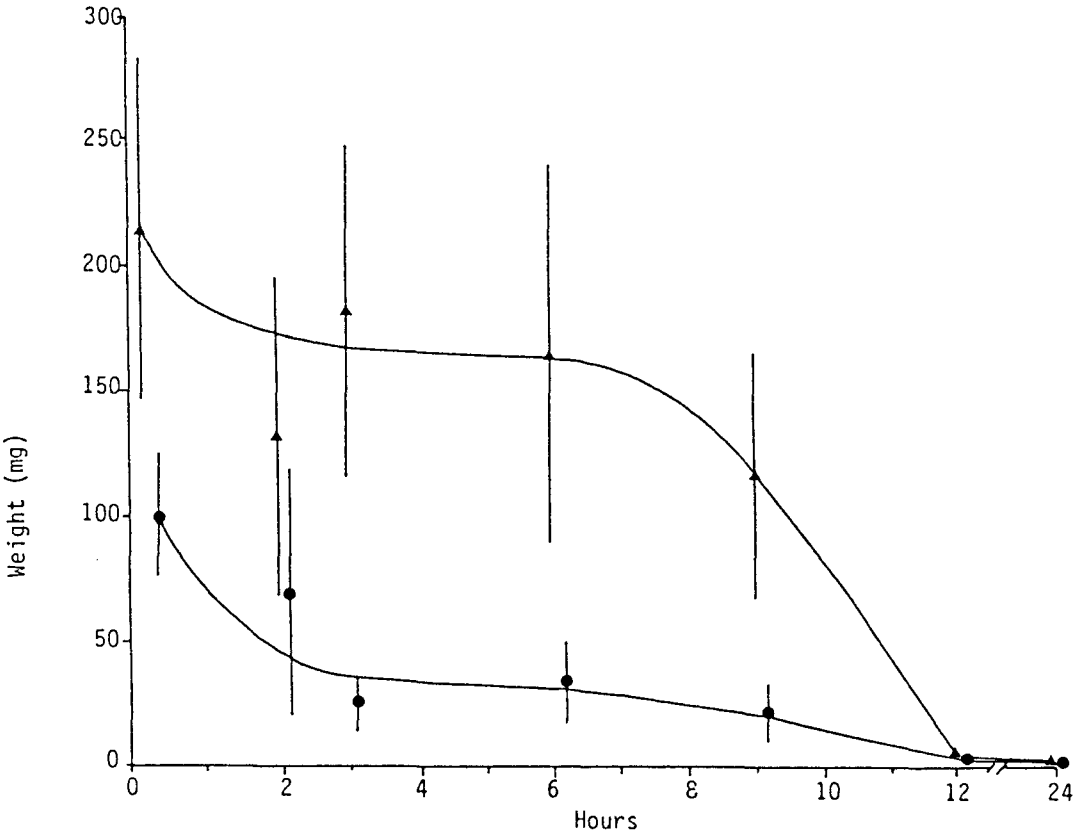


Fig 18. Ammount of flesh and shell remaining in the foregut of O. catharus relative to hours of digestion time. Triangles represent shell (n=35) circles flesh (n=35). Error bars represent 95% confidence limits. Curves fitted by eye.

DIET ANALYSES, SAMPLE SITES AND COLLECTION DATES

Paddle Crab Collections

Samples of paddle crabs used for diet analyses were collected between April 1985 and March 1986, from three subtidal soft bottom sites at Little Akaloa, South Brighton Beach and Taylors Mistake, Canterbury (Fig.19). Four collection methods were used depending on the location and the catchability of the crabs. An otter trawl with 30 mm net mesh and 15 mm cod end mesh was used at Brighton Beach and Taylors Mistake, towed behind a Haines Hunter powered by a 140 hp Johnston outboard. A beam trawl was the most successful capture method used at Little Akaloa, towed behind a 4 m Parker Craft powered by a 25 hp Johnston Seahorse. Crabs pots with fish bait protected in 0.25 mm mesh bags were used at Little Akaloa when trawling failed to catch sufficient crabs for gut analyses purposes. SCUBA was used on two occasions when crabs could not be caught by either trawling or potting.

Little Akaloa was sampled 13 times during 11 and 12 June(4), 16 July(1), 26 Sept(2), 12 October(2), and 2 December(2) and 6 March(2) 1986 (Table 15). Little Akaloa was characterised by having an unstable population of crabs, therefore, adequate numbers of foreguts required for diet analyses were not always available. In these cases, collections were grouped together for convenience of analysis. Eight South Brighton Beach trawls were made within a distance of 2 km from the surf zone on 15 April(1), 3 July(1), 17 October(2), and 2 December(2) 1985 and 7 March(2) 1986 (Table 16). Trawl times were between 35 and 45

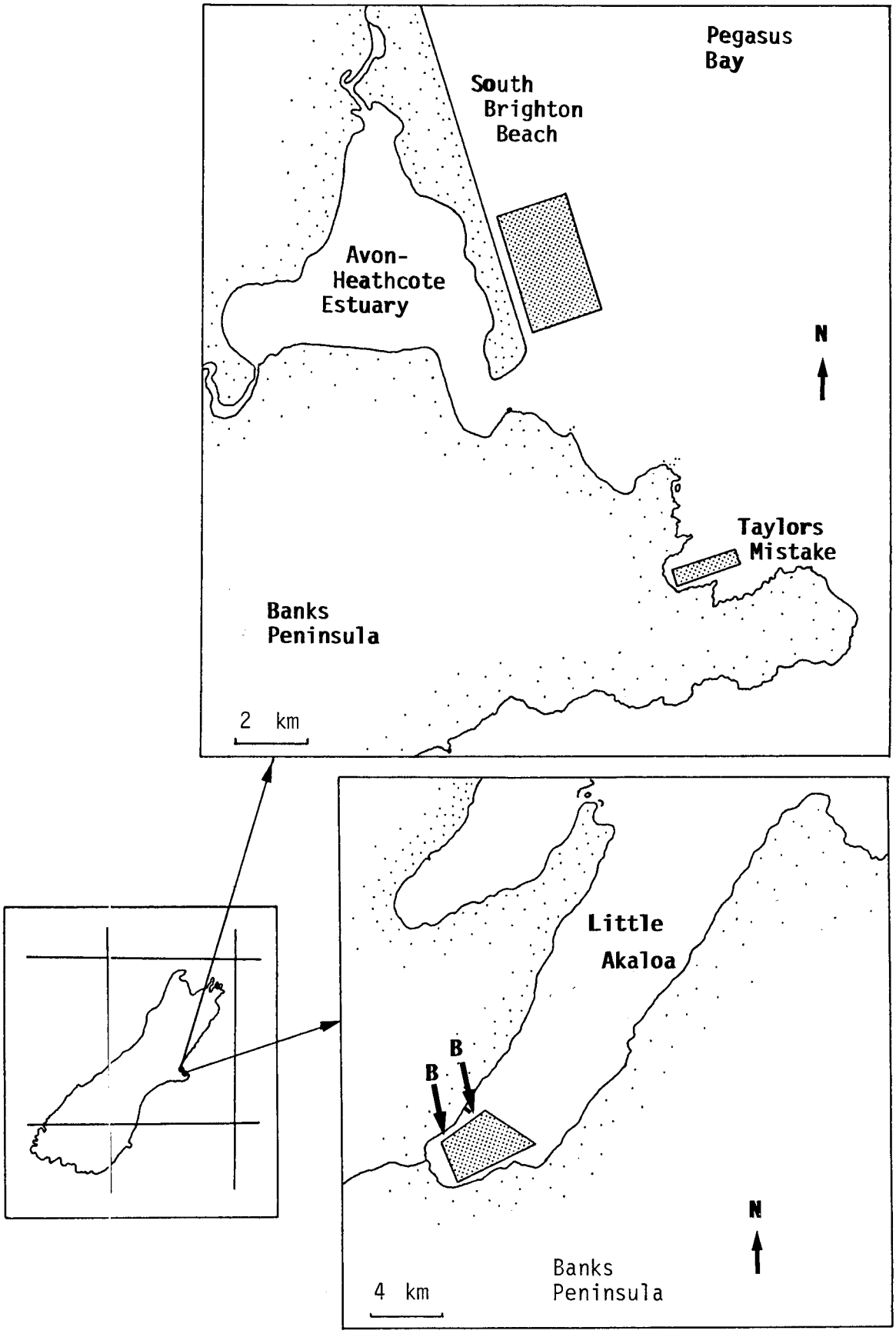


Fig 19. Sample locations around Banks Peninsula. Stippled areas represent crab and epibenthic collection areas, arrows represent benthic sample sites.

Table 15. Collections of O. catharus during the 1985-86 year from Little Akaloa.

Date	Sample times	No of crabs coll.	High Tide	Water Temp	Sample Methods	Weather Conditions	Pre-Sample Weather
11 June 1985	1200	69	1200	12.5°C	Beam trawl	No swell, light sea, Northerly wind.	No storms, little wind, northerly air stream.
	1700	57					
12 June 1985	2400	2					
	700	106					
16 July 1985	1200	69	1300	10°C	Beam trawl Potting with bait	0.5m Northeast swell, light sea, light Northeast wind.	
26 September 1985	700	14	1400	10°C	Beam trawl Potting	0.75m easterly swell, light sea, slight Northeast wind.	Calm for week previous, northerly storm 2 weeks earlier.
	1400	25					
12 October 1985	1400	21	1626	11.5°C	Potting	No swell, no sea, light Northeast wind.	
6 December 1985	1000	48	1200	12.5°C	Beam trawl	No swell, little sea, light Northeast wind, clear.	Southerly air stream.
	1900	73					
6 March 1986	1000	1	1200	17°C	Beam trawl Potting Diving	No swell, no sea, light Northeast wind, clear.	Weather calm, no large swells.
	1700	2					

Table 16. Collections of O. catharus during the 1985-86 year from Brighton Beach and Taylors Mistake*

Date	Sample times	No of crabs coll.	High Tide	Water Temp	Sample Methods	Weather Conditions	Pre-Sample Weather
15 April 1985	900	78	1300	16°C	Otter trawl	No swell, calm, light south east wind, clear.	No storms, southerly air stream.
	1100*	14					
3 July 1985	700	88	500	11.5°C	Otter trawl	No swell, clam, light Northwest wind, clear.	Northerly air stream, no storms.
17 October 1985	900	66	600	11.5°C	Otter trawl	0.5m Northeast swell, no sea, overcast.	Calm and clear for previous 2 weeks.
	930	33					
	1000*	36					
2 December 1985	930	72	900	12.5°C	Otter trawl	1.0m east swell, no sea, light southerly drizzle.	Calm for week previous.
	1000	62					
	1030*	72					
	1100*	39					
7 March 1986	930	72	600	17°C	Otter trawl	1m easterly swell, no sea, light southerly, raining.	Northerly storm 2 weeks previous.
	1000	71					
	1100*	43					

* Taylors Mistake samples.

minutes and captured 60-100 crabs. This was considered sufficient for stomach analyses purposes (Williams, 1981; Appendix 1). Five Taylors Mistake trawls were made within a distance of 1.5 km from the beach during 15 April(1), 12 October(1), and 2 December(2) 1985 and 7 March(1) 1986 (Table 16). Samples at Brighton Beach and Taylors Mistake were taken on high tides between 7 am and 10 am. Little Akaloa samples were taken during early morning and evening high tides. Midday and midnight trawls were also taken at Little Akaloa in June 1985. At all sites, weather and sea conditions were recorded for the two weeks previous to collections and during collections.

Foregut Examination

On capture, the crab carapace was punctured followed by immediate preservation in 10% formalin. In the laboratory, crabs were measured, sexed and sorted into two size groups: year class 1, 0 to 65 mm and year class 2 and 3, 65.1 to 120 mm carapace width (CW). The condition of the carapace was noted and stomachs removed and placed in 10% formalin in individually labelled vials. Before the foreguts were opened, fullness was ranked visually on a scale of 1-7, where 1 denoted empty, 2 trace to 10%, 3 as 25%, 4 as 50%, 5 as 75%, 6 as full and 7 represented a distended foregut. Foregut contents were transferred to 70% alcohol and examined under a dissecting microscope. Food freshness or the state of digestion, was ranked on a scale of 1-4, where 1 represented fresh flesh or whole animals collected within one hour of prey consumption, 2 as flesh partially digested or fine carapace present (1-4 h), 3 as flesh completely

digested, fine carapace present but in poor condition (4–6 h), and 4 as hard carapace, bones, scales and chelae only present (6–12 h). Contents were often shredded making identification difficult, however, identification to family, genus and sometimes species was possible by comparing characteristic body parts with whole animals retained from trawls. Individual counts of organisms and estimates of percentage volume of each prey type in the foregut were also taken. The shredded, often paste nature of the gut contents made separation of individual items for weighing impossible. Total stomach contents for each sub-sample were dried to a constant weight at 65°C.

Analyses of Diet Data

For each sample of crab foreguts, percent numerical composition (NC) was calculated using:

$$\frac{\text{Number of individuals of species A}}{\text{Number of individuals of all species.}} \times 100$$

Percentage volumetric composition replaced gravimetric composition (Pinkas et al., 1971), as individual prey weights could not be obtained. Volumetric composition was calculated using the Program GUTSACHE writen by C.L. M^{c}Clay and stored at the Zoology Department, University of Canterbury. Volumetric composition (VC) and fullness of each stomach was analysed in the form:

$$\frac{\text{(relative volume . fullness) species A}}{\text{(relative volume . fullness) all species.}} \times 100$$

Percent frequency occurrence (FO) was calculated using the equation:

$$\frac{\text{Number of foreguts containing species A}}{\text{Number of foreguts containing food.}} \times 100$$

Numerical composition, volumetric composition and frequency occurrence were used separately on occasion and were also incorporated into the Index of Relative Importance (IRI).

Two statistical procedures were used to analyse the diet of the paddle crab. Kruskal-Wallis test (Zar, 1974), is a non-parametric statistic used to test the null hypothesis that two or more samples are not significantly different. This test was used to compare frequency occurrence of prey in the diet of the two size classes over the day, month, season and sample sites. If the calculated P-value was less than 0.05 the null hypothesis was rejected. Diets found to be similar (> 0.05) were combined and presented seasonally as: autumn (March, April); winter (June, July); spring (September, October); and summer (December).

The degree of overlap or similarity between species present in the environment with those found in the diet of O. catharus was calculated using the Pianka (1973) equation:

$$O_{jk} = O_{kj} = P_{ij}P_{ik} \; / \; P_{ij}^{2} \; P_{ik}^{2}$$

where P_{ij} and P_{ik} are the proportions of the ith resource used by

the jth and kth groups. The equation is convenient as it gives a single overlap value for each comparison; it can never generate values less than 0 or greater than 1. Complete separation of available food and that present in the diet of crabs will tend towards values approaching 0, while values approaching 1 indicate similarity. A value greater than 0.60 is considered to be significant (Zaret and Rand, 1971). A high value would suggest that crabs select particular food types from those available in the environment.

The following 19 categories were used to group organisms found in the benthos, epibenthos and crab diet.

1 Gastropods

2 Dosinia subrosea

3 Tellina sp.#1

4 Nucula hartvigiana

5 Tellina sp#2

6 Bivalves

7 Pectinaria sp.

8 Polychaetes

9 Mysid sp.

10 Amphipods

11 Zenobiana tubicola

12 Cumaceans

13 Ovalipes catharus

14 Hymenosomatids

15 Decapods

16 Echinoderms

17 Teleosts

18 Algae

19 Unidentified animal matter

No quantitative measurement of plant material or paddle crab numbers were possible from benthic or epibenthic collections, therefore, these categories were excluded from diet overlap calculations. For each site, all data for the year were analysed as a combined sample, while seasonal comparisons at Little Akaloa were made by combining samples taken throughout the day. Comparisons between the two size groups of crabs (year 1, 0-65 mm CW; year2-3, 65.1-120 mm CW) used combined data for each site. The factors affecting paddle crab diet were analysed with respect to location, prey availability, diel activity, sex, ovigerous condition, carapace condition and temperature.

RESULTS OF DIET STUDY

Identification of Food from the Foregut

The fragmentous action of the mouth parts, chelipeds and gastric mill of the paddle crab Ovalipes catharus, made specific identification of prey and its occurrence in the diet difficult. The presence of hard parts, however, enabled soft indistinguishable parts to be identified (Table 17). Each part, if not immediately identifiable was compared with prey items collected from the field. Many food items, including amphipods, isopods, mysids, bryozoans and decapods were, however, ingested whole or in large pieces allowing identification down to species level. Often food was masticated into a paste and was therefore beyond recognition. On these occasions prey items could often be identified by the presence of associated hard parts. Paddle crab foreguts contained inorganic material including sand, silt and shell fragments and items of human extraction such as string and rope fragments. Some items present in the foregut of O. catharus originated from the stomachs of prey consumed by crabs. They included nematodes and small crustaceans. These items were not part of paddle crab diet and were not included in calculations.

Natural Diet

A total of 1233 paddle crab foreguts were examined, 487 from Little Akaloa, 542 from South Brighton Beach and 204 from Taylors Mistake (Table 18). The percentage of crabs with empty foreguts was 28.6% at Little Akaloa, 43.3% at Brighton Beach and 44.2% at Taylors Mistake. Mean sediment content per foregut of crabs

FOOD TYPE	Characteristic Parts Used for Identification
Polychaeta	Setae, sections of animal, jaws (Nereidae, Eunicidae), feeding brushes (Pectinaria).
Amphipoda	Whole animal, segments, gnathopods, appendages.
Isopoda	Whole animal, telson, appendages, antennae.
Bivalvia	Whole shell, shell fragments, hinges, operculum, umbone, flesh.
Cumacea	Whole animal, large sections of exoskeleton.
Decapoda	Chela, carapace, carapace spines, flattened dactylus with setae (O. catharus), gill fragments, limb fragments, eyes.
Hymenosomatid	Rostral spines, tube legs, chela, fragments, stalked eyes.
Teleostei	Scales, oil droplets, whole body, eye lenses, bones, otoliths, vertebrae, fin rays.
Echinodermata	Pieces of test, ossicles.
Ophiuroidea	Pieces of leg, pieces of test.
Bryozoa	Small to large sections of whole animals.
Plants	Small pieces of leaf and stalk.

Table 17. Characteristic parts used to identify of food items present in the foregut of Ovalipes catharus

Measurement	Little Akaloa	Brighton Beach	Taylors Mistake
Carapace width range (mm)	21.8-107	31.6-123	34.5-112
Mean carapace width (mm)	62.3	76.9	68.9
Number of crabs collected	487	542	204
Percent empty foreguts	28.6	43.3	44.2
Percent sediment per foregut	25.9	13.1	11.8
Mean foregut fullness (1-7)*	2.87	2.96	2.42
Mean flesh freshness (1-4)+	3.09	2.29	2.38
Number of prey items per crab	1.93	3.54	1.75
Number of taxa per crab	1.21	1.62	1.47

Table 18 Combined sample and size class data for O. catharus collected from each of the 3 sample sites. Calculations include crabs with empty foreguts. * scale represents foreguts: 1 = empty to 6 = full and 7 = distended; + scale represents: 1 = undigested or whole food items, eaten within 1 hour of crab capture, 4 = food well digested, consumed 6-12 hours previous to collection.

collected at Little Akaloa (25.9%) was twice that recorded for the two other sites. The number of prey items per crab foregut (3.54), number of prey taxanomic categories (1.62), and gut fullness (2.96) was highest for crabs collected at Brighton Beach.

A total of 39 species were eaten by paddle crabs (Table 19), 29 from Little Akaloa, 23 from Brighton Beach and 22 from Taylors Mistake. Sixteen species were common to crabs from all locations and 24 species were represented at two sites. All 39 dietary species were recorded from benthic and epibenthic collections (see faunal collections section). Additional to species present in crab diet, 58 species were recorded from faunal collections made during the year. Polychaetes, dominant in the environment were under-represented in crab diet, with only 5 out of the total of 25 possible species being eaten. Crab diet consisted of 7 species of Bivalvia, 7 Amphipoda, 5 Polychaeta, 4 Decapoda and a few representatives of Hydrozoa, Gastropoda, Mysidacea, Isopoda, Cumacea, Pycnogonida, Echinodermata,Insecta, Teleostei and Phycophyta.

Paddle crab diet was calculated using Index of Relative Importance (IRI) tables. An example is shown for combined year class 1 crabs (0-65 mm carapace width) collected at Taylors Mistake (Table 20). Bivalvia and similar groups include only unidentified individuals and excludes species such as Dosinia subrosea and Nucula hartvigiana. Percent numerical occurrence and volumetric composition data for each sample site and crab size class were plotted above and below the x axis, represented as cumulative frequency occurrence (Figs 20,21,22). The

Table 19. List of organisms found in the foreguts of Ovalipes catharus, collected 1985-86

PHYLUM : MOLLUSCA

Class Gastropoda
*+! Xymene Iredale, 1915

Class Bivalvia
\+ Divaricella sp. Iredale, 1936
*+! Dosinia subrosea (Gray, 1935)
* Mactra discors Gray, 1935
*+! Nucula hartvigiana Pfeiffer, 1864
*+! Perna caniculanus
*+! Tellina (Macomona) liliana Iredale, 1915
*+! Tellina sp. Mrch, 1853

PHYLUM : ANNELIDA

Class Polychaeta
* Eunicidae Salvigny, 1818
* Glyceridae Grube, 1850
*+ Nereidae Johnston, 1845
* ! Pectinaria sp. Savigny, 1818
* Sabellidae sp. Malmgren, 1867

PHYLUM : ARTHROPODA

Class Crustacea
Order Mysidacea
*+! Mysid sp.
Order Cumacea
*+! Diastylidae
Order Amphipoda
*+! Allorchestes sp. Dana, 1852
Amphipod sp.#1
Amphipod sp.#2
Amphipod sp.#3
Amphipod sp#4
*+! Atylus taupo Chilton, 1923
! Phoxocephalid sp.
Order Isopoda
* Aegid sp.
*+! Zenobiana tubicola (Thompson)
Order Decapoda
* Crangon sp.
+! Halicarcinus pubescens (Dana, 1851)
*+! Hymenosoma depressum Jacquinot, 1853
*+! Ovalipes catharus (White, 1843)

Class Pycnogonida
* Achelia dohrni (Thomspon, 1884)

Phylum Echinodermata

+! Class Echinoidea
*+ Class Ophiuroidea

Phylum Insecta
*+

Phylum Teleostei

*+! Pseudophycis bachus (Bloch & Schneider, 1801)
* Rhombosolea sp. Hutton

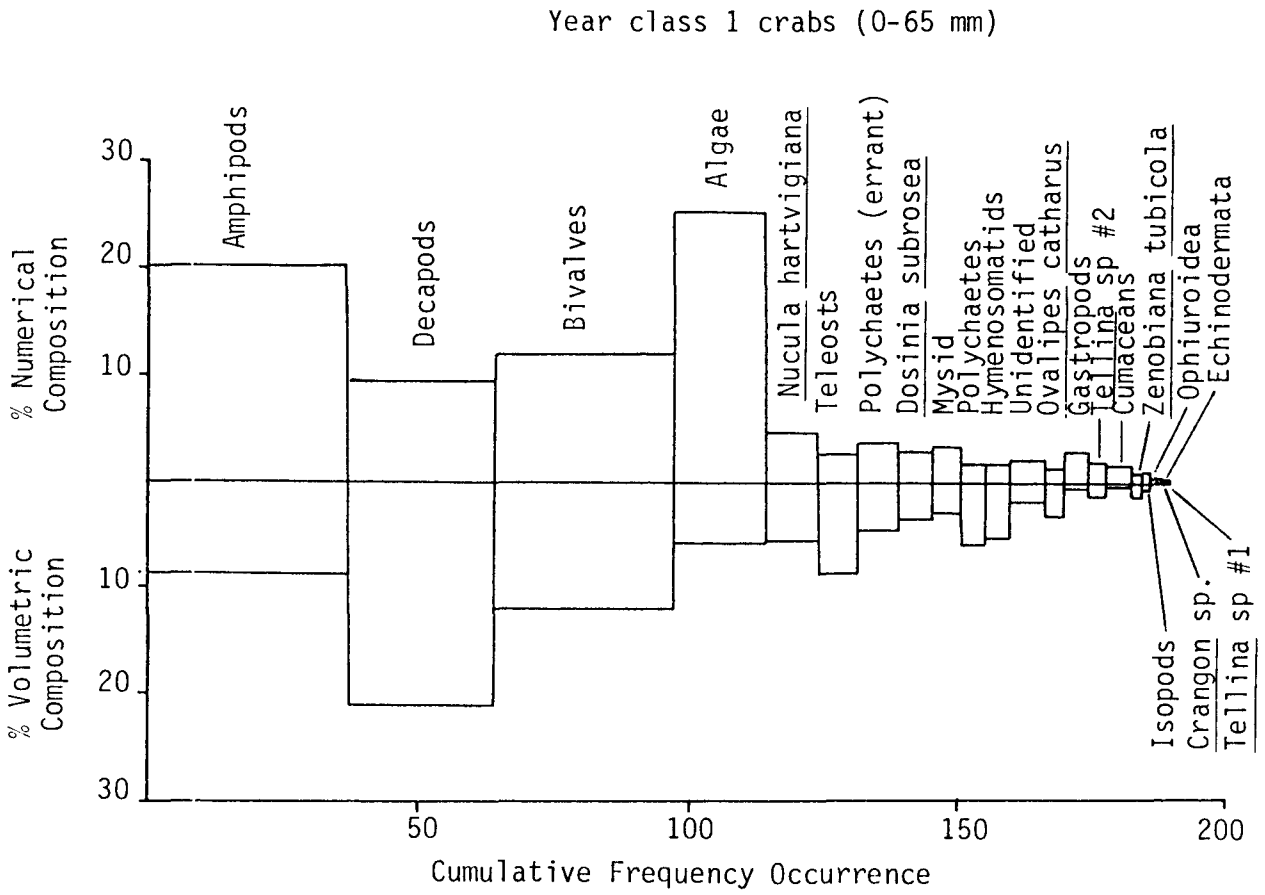
Phylum Phycophyta

*+! Chlorophyceae
*+! Phaeophyceae
*+! Rhodophyceae

Recorded from: * Little Akaloa; + Brighton Beach; ! Taylors Mistake

PREY ITEM	% FREQ. OCCUR.	% NUM OCCUR.	% VOL. COMP.	PREY IRI	% OF TOTAL IRI
Tellina sp # 2	40.68	30.10	28.89	2277.67	56.56
Cumacean	20.34	24.50	6.90	638.68	15.86
Bivalvia	16.95	6.55	9.28	268.32	6.66
Hymenosomatids	13.56	4.40	11.56	216.42	5.37
Ovalipes catharus	11.86	3.06	14.57	209.09	5.19
Dosinia subrosea	15.25	4.44	2.99	113.31	2.81
Teleostei	8.47	2.20	10.38	106.55	2.65
Decapoda	10.17	2.60	5.44	81.77	2.03
Mysid sp	3.39	5.68	2.50	27.73	.69
Hymenosoma pubescens	3.39	1.30	3.46	16.14	.4
Hymenosoma depressum	5.08	1.30	1.73	15.39	.38
Amphipoda (benthic)	5.08	1.30	.59	9.60	.24
Gastropoda	5.08	1.30	.49	8.99	.22
Tellina sp # 1	3.39	1.75	.55	7.80	.19
Nucula hartvigiana	3.39	1.30	.94	7.59	.19
Echinodermata	3.39	.87	1.30	7.36	.18
Unidentified	3.39	.87	.63	5.09	.13
Pectinaridae	3.39	.87	.39	4.27	.11
Amphipoda (epibenthic)	3.39	.87	.08	3.22	.08
Pseudophycis bachus	1.70	.44	.31	1.28	.03
Perna canaliculus	1.70	.44	.31	1.28	.03

Table 20 Example of IRI Table with percent frequency occurrence, percent numerical composition, percent volumetric composition, prey IRI and percent of total IRI for 59 small crabs collected over the year at Taylors Mistake. Prey values are not repeated i.e. "Decapoda" includes only unidentified decapods.



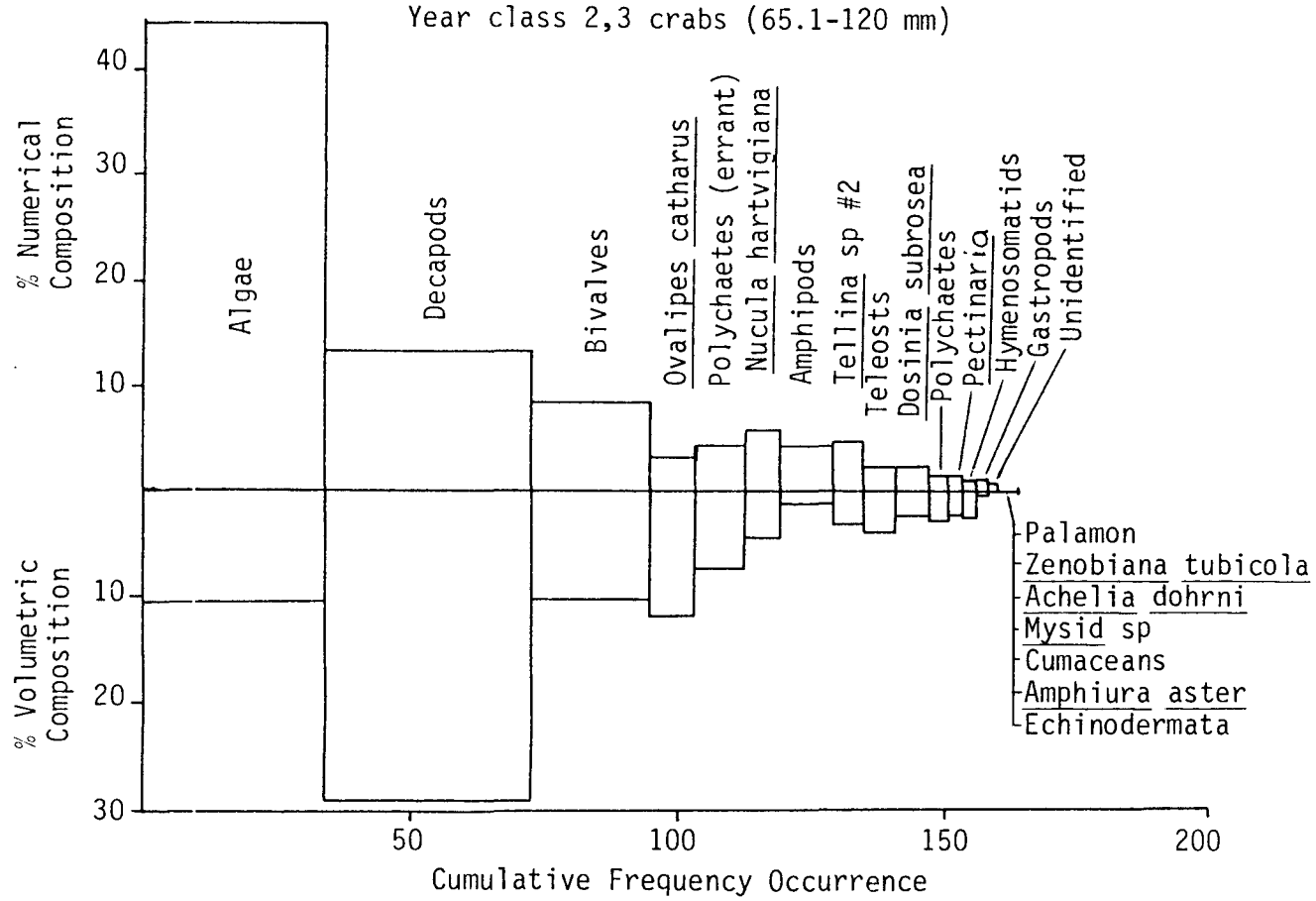


Fig 20. Plot of IRI (Index of Relative Importance) for combined samples of 0-65 mm and 65.1-120 mm crabs collected from Little Akaloa. Total area of each rectangle represents total IRI for that item in the diet of O. catharus.

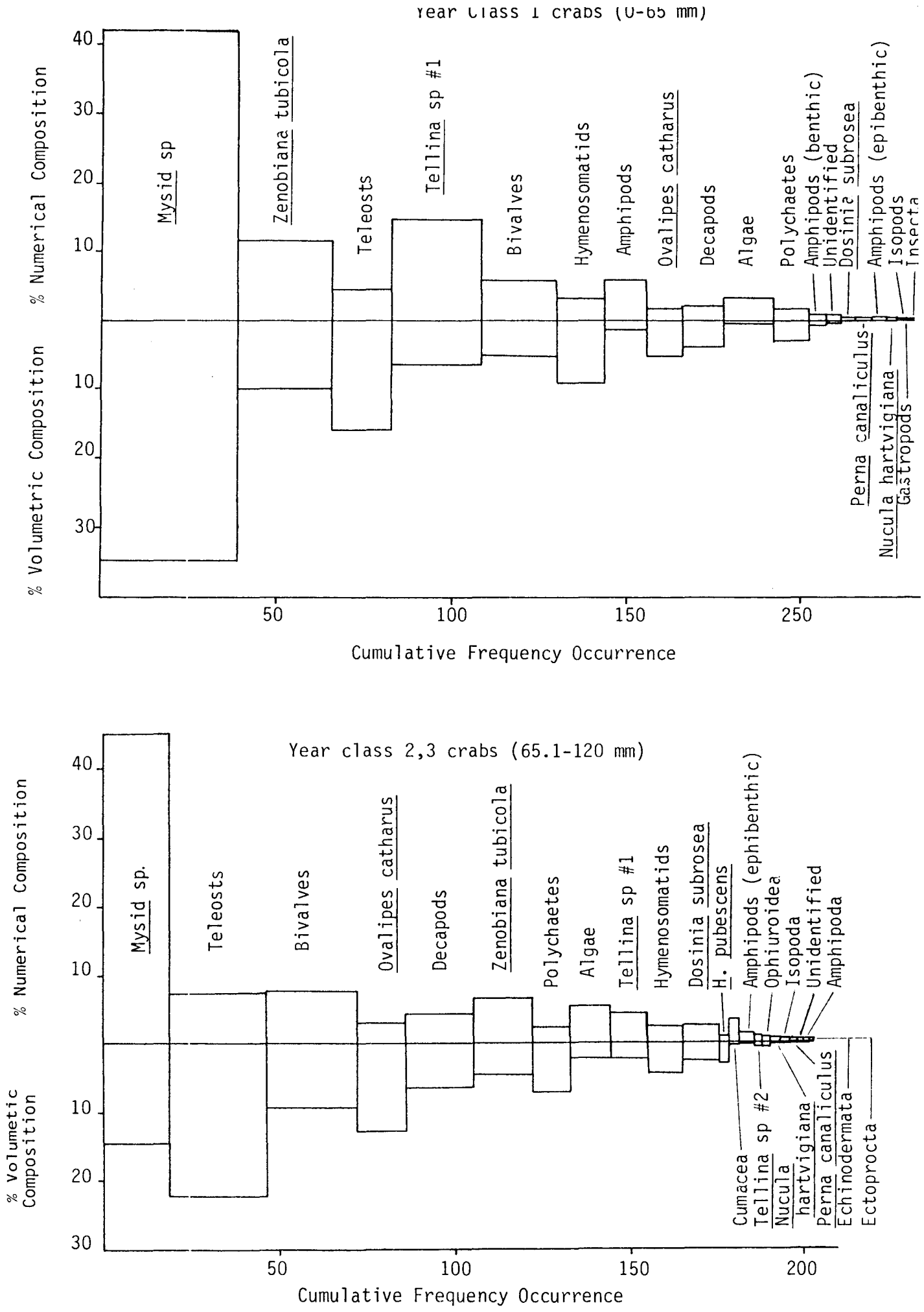
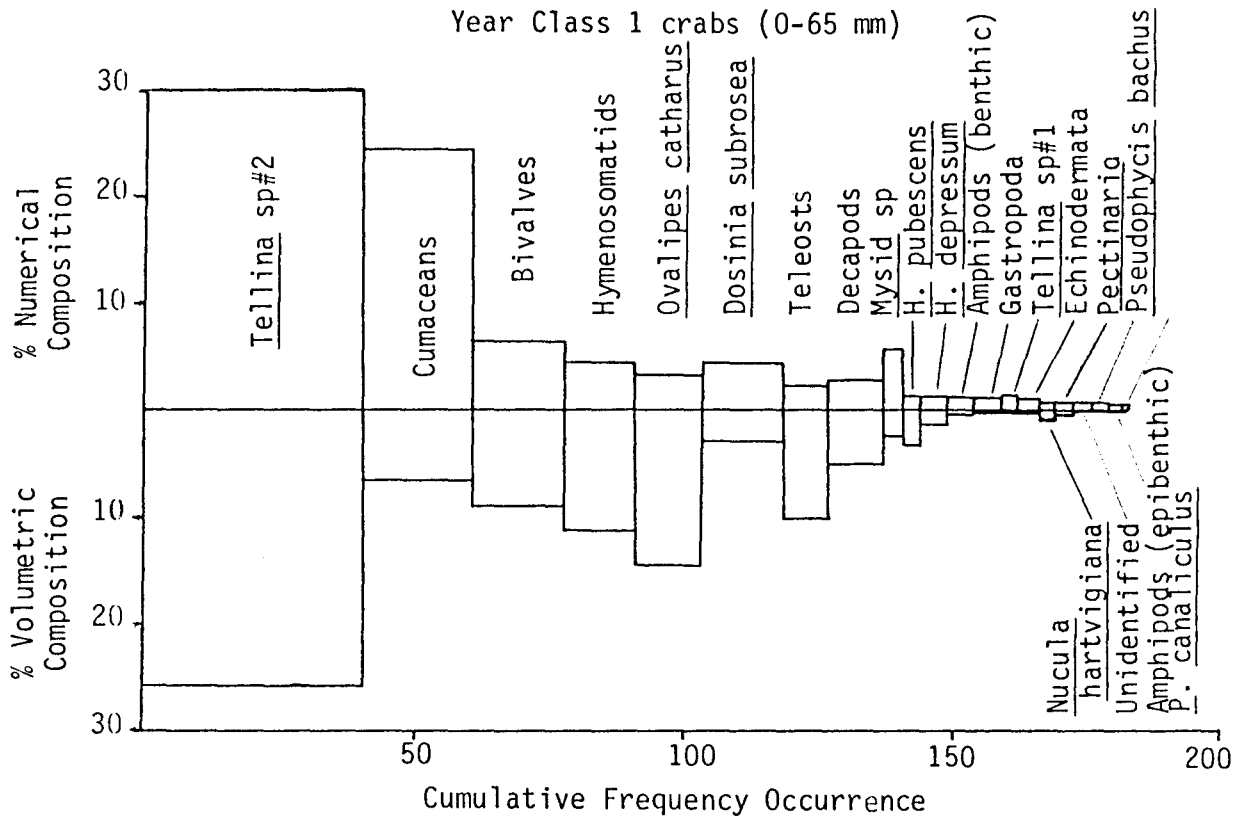


Fig 21. Plot of IRI for combined samples of 0-65 mm and 65.1-120 mm crabs collected from Brighton Beach, Total area of rectangle represents total IRI for that item in the diet of O. catharus.



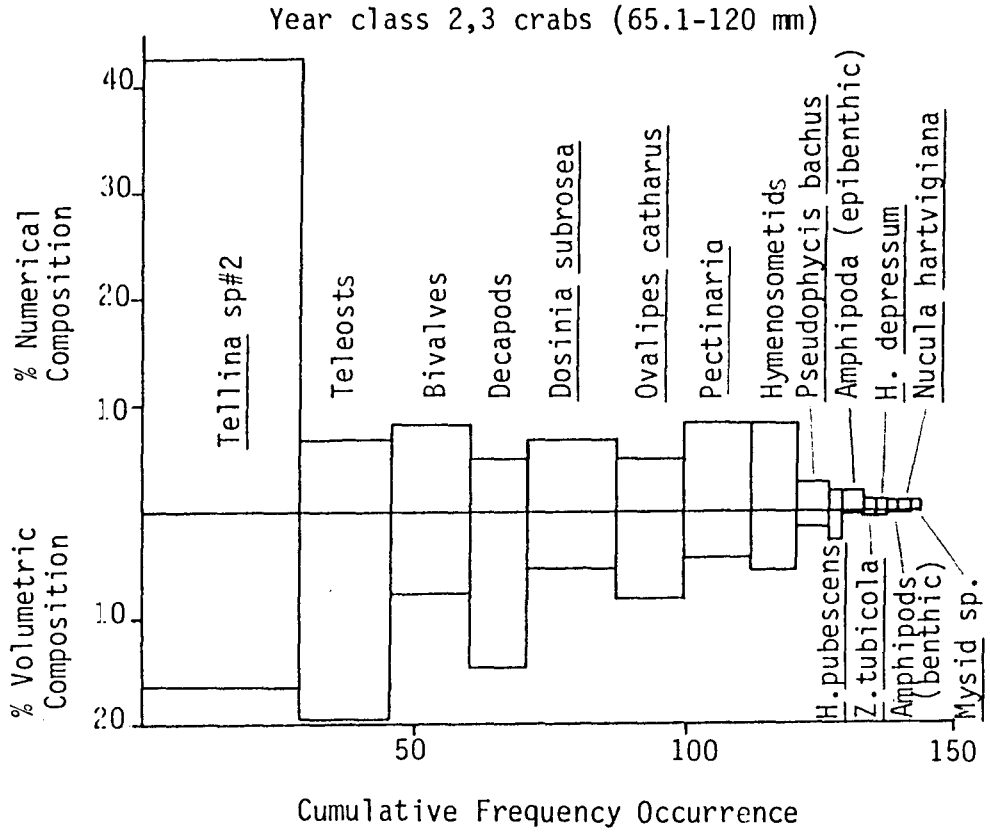


Fig 22. Plot of IRI for combined samples of 0-65 mm and 65.1-120 mm crabs collected from Taylors Mistake. Total area of rectangle represents total IRI for that item in the diet of O. catharus.

Location	Size class	Number of crabs in sample	Gut dry weight per crab (mg)	Percent Total IRI				
				Crustaceans	Bivalves	Fish	Three most important taxa	
Little Akaloa	0 - 65mm	258	7.10	54.30	25.29	2.38	Amphipods	28.89
							Decapods	22.69
							Bivalves	21.32
Little Akaloa	65.1-120mm	229	8.95	41.13	12.47	0.87	Algae	42.32
							Decapods	36.68
							Bivalves	9.18
Brighton Beach	0 - 65mm	130	12.18	76.35	10.98	10.60	*Mysid* sp.	57.59
							Zenobiana tubicola	10.72
							Teleosts	10.60
Brighton Beach	65.1-120mm	412	16.47	53.21	16.57	24.29	*Mysid* sp.	32.13
							Teleosts	24.29
							Bivalves	12.60
Taylors Mistake	0 - 65mm	103	8.4	30.24	66.44	2.68	*Tellina* sp. 2	56.56
							Cumaceans	15.86
							Bivalves	6.66
Taylors Mistake	65.1-120mm	101	11.39	15.41	64.35	15.47	*Tellina* sp. 2	51.38
							Teleosts	13.01
							Bivalves	6.97

Table 21 Major food categories in the diet of *O. catharus* for combined samples collected from Little Akaloa, Brighton Beach and Taylors Mistake.

importance of Crustacea, Bivalvia, Teleostei or Algae in crab diet is summarised for the combined years results for each site and year class in Table 21.

The most important components in the diet of the paddle crab varied between sites throughout the year (Table 21). In all cases, 2-4 categories dominated crab diet (Figs 20,21,22). Overall, crustaceans were the most important food for small crabs (54.3%) and large crabs (41.1%) at Little Akaloa. At Brighton Beach crustaceans comprised 76.4 and 53.2% for small and large crabs respectively. Amphipods and decapods were the most important crustaceans at Little Akaloa, while mysids and the isopod Zenobiana tubicola where the major species at Brighton Beach (Table 21). Algae were the major dietary component (42.3%) for larger crabs from Little Akaloa with decapods and bivalves, the next two most important groups (36.7% and 9.2%) respectively (Fig.20). For smaller crabs from Little Akaloa, the most important component of the diet throughout the year were amphipods (28.9%) followed by decapods (22.7%) and bivalves (21.3%). In contrast, for crabs collected from Taylors Mistake, bivalves comprised 66% and 64% of the diet for the two size classes followed by cumaceans (15.8%) and bivalves (6.76%) in small crabs and teleosts (13.01%) and bivalves (6.97%) in large crabs (Fig.22). Comparison of combined crab diets between Taylors Mistake and Brighton Beach ($H=6.53$, $P < 0.025$) and Little Akaloa ($H=3.71$, $P < 0.005$) were significantly different. This was probably due to bivalve dominance at Taylors Mistake and crustacean dominance at the other two sites . No significant difference for crab diets was recorded between Little Akaloa and

Brighton Beach (H=1.5, P > 0.2).

Paddle Crab Diet at Little Akaloa

Crustaceans were the most important food in paddle crab diet during June (early winter) at Little Akaloa (Table 22). They formed 57.2-69.6% IRI and were followed in importance by bivalves (5.4-22.5%). During July (mid-winter), crustaceans (17.6%) were replaced in crab diet by plant material (81.7%) (Table 22). Bivalves, polychaetes, decapods and echinoderms represented less than 5% of the diet. In September (spring), bivalves represented 52.5% of small and 28.8% of larger crab diet. Amphipods in large crab diet represented 21-23% Bivalves (31%) and crustaceans were the most important groups in crab diet during October (late spring), however, algae (38.7%) was the single most important group. For December (summer), bivalves formed 53.2- 88% of the diet with crustaceans comprising between 26.9% and 54%. The bivalves Dosinia subrosea, Nucula hartvigiana and Tellina sp#2, and the decapods O. catharus and hymenosomatids were the major groups responsible.

Table 23 summarises the feeding data collected from Little Akaloa throughout 1985-86. The percentage of non-feeding crabs was lowest in the evening sample (1.75%) and highest for crabs collected in the afternoon spring sample (48%). Percent empty foreguts were similar for all collections at Little Akaloa (21.4-27.4%). Foregut fullness values also remained relatively constant over the sample period (2.24-3.08%) The number of prey items per crab foregut was highest in evening collections during spring (3.71). Feeding data from Little Akaloa suggest that prey

Date	Time	Size Class	Gut Dry Weight Per Crab (mg)	Percent Total IRI				
				Crustacean	Bivalva	Algae	Three Most Important Taxa	
11 June 85	1200	0-65mm	5.69	57.5	18.6	17.4	Decapods Bivalves Algae	48.25 18.44 17.4
11 June 85	1200	65.1-120mm	24.19	69.6	5.44	4.93	Decapods Polychaetes Bivalves	66.6 16.44 5.44
11 June 85	1700	0-65mm	5.94	60.8	18.01	13.64	Amphipods Decapods Algae	34.15 26.26 13.64
2 June	700	0-65mm	1.59	57.15	22.51	13.56	Amphipods Bivalves Decapods	36.97 22.51 17.77
12 June	700	65.1-120mm	1.41	41.85	5.74	42.92	Algae Decapods Polychaetes	42.92 28.97 9.5
16 July	1400	65.1-120mm	8.93	17.59	0.57	81.72	Algae Decapods O. catharus	81.72 16.13 1.45
26 Sept	700	0-120mm	8.0	39.20	52.52	0	Bivalves Amphipods Decapods	52.52 21.44 8.02
26 Sept	1500	0-120mm	5.89	51.26	26.8	21.26	Bivalves Amphipods Algae	26.8 23.01 21.26
12 Oct	1400	0-120mm	9.12	27.96	30.97	38.65	Algae Bivalves O. catharus	38.65 29.51 18.6
6 Dec	1000	0-65mm	61.82	9.29	88.01	0	Dosinia subrosea Tellina sp#2 Decapods	80.0 7.26 3.26
6 Dec	1000	65.1-120mm	2.71	33.68	53.18	1.67	Decapods Bivalves Nucula hartugiana	29.63 18.54 15.92
6 Dec	1900	0-65mm	5.5	26.85	55.94	0	Bivalves Tellina sp#2 Hymenosomatid	21.38 17.32 16.9
6 Dec	1900	65.1-120mm	9.35	54.04	30.75	0.29	Decapods Bivalves O. catharus	43.63 12.39 9.3

Table22. Major taxanomic categories and food types present in the diet of O. catharus for samples collected at Little Akaloa, 1985.

Measurement	Autumn				Winter	Early-Spring		Spring	Summer	
	Daybreak	Midday	Evening	Midnight	Midday	Daybreak	Afternoon	Afternoon	Morning	Afternoon
Carapace width range (mm)	32.8-82	33.8-102	33.2-80	45.8-47	67.4-100	42-91.8	56.8-100	53.7-101	27.8-86	32.2-107
Mean carapace width (mm)	52.9	58.7	46.5	46.4	80	69.1	69.1	68.8	65.8	66
Number of crabs collected	106	69	57	2	69	14	25	21	48	73
Percent empty foreguts	27.4	23.2	1.75	50	23.2	21.4	48	23.8	25	42.5
Percent sediment per foregut	41.3	46.6	30.2	-	27.3	19.3	17.6	20.5	15.8	14.4
Mean foregut fullness (1-7)*	2.85	2.97	3.7	-	2.29	2.86	2.24	2.9	3.08	2.51
Mean flesh freshness (1-4)+	NA	NA	NA	NA	4.21	2.56	2.62	3.23	3.1	2.85
Number of prey items per crab	1.31	1.83	3.46	-	2.39	3.71	.92	1.43	2.46	1.29
Number of taxa per crab	0.93	1.3	2.03	-	1.28	1.43	.92	1.0	1.56	1.1

Table 23 Combined sample and size class data for O. catharus collected from Little Akaloa. Calculations include crabs with empty foreguts. * scale represents foreguts: 1 = empty to 6 = full and 7 = distended; + scale represents: 1 = undigested or whole food items, eaten within 1 hour of crab capture, 4 = food well digested, consumed 6-12 hours previous to collection.

availability and feeding activity of crabs remained constant over the entire sampling period. This was reflected in foregut fullness, flesh freshness, number of prey and prey taxa found per crab foregut.

Paddle Crab diet at Brighton Beach

Throughout the 1985-1986 year, crustaceans, bivalves and teleosts formed the three major components of the diet of crabs from Brighton Beach (Table 24). Algae, important at Little Akaloa formed less than 2% IRI at Brighton Beach. Crustaceans were the most important items in crab diet during autumn (1985), winter and spring, for larger crabs during summer, and smaller predators during autumn (1986). Bivalves were important in small crab diet during summer (42.2%) and large crab diet in autumn (43.7%). Teleosts were important in paddle crab diet during spring (17.1-18.2% IRI), summer (7.2-30.5%) and autumn (large crabs, 15.05%). During spring, highest percent dry weights per crab foregut were recorded, suggesting high levels of feeding activity (Table 24). Dry weights of food contained within the foregut declined through summer, increased in autumn, and declined again during winter (Table 25). The percentage of crabs with empty foreguts varied from 9.1% in spring to 80.5% in winter. During winter, the large proportion of crabs with empty foreguts was accompanied by low foregut fullness values (1.6), number of prey (0.24) and prey categories per stomach (0.24). During spring only 9.1% of crab foreguts were empty, while values of mean stomach fullness 75-100%, number of prey items per stomach 13.4 and prey taxa 3.6 were high suggesting intense

Date	Time	Size Class	Gut Dry Weight per Crab (mg)	Percent Total IRI				
				Crustaceans	Bivalves	Fish	Three Most Important Taxa	
15 April	900	0-65mm	9.75	58.25	41.72	0	Tellina sp#1	41.27
							Zenobiana tubicola	37.34
							Amphipods	11.18
15 April	900	65.1-120mm	8.47	54.25	42.99	0.42	Zenobiana tubicola	48.52
							Tellina sp#1	41.28
							O. catharus	3.26
3 July	700	0-120mm	5.88	80.1	7.53	4.69	Decapods	49.95
							O. catharus	30.15
							Bivalves	7.53
17 Oct.	900	0-120mm	13.31	51.16	21.42	17.11	Cumaceans	29.49
							Bivalves	21.06
							Teleosts	17.11
17 Oct.	930	0-65.1mm	17.09	84.45	0.46	13.73	Mysid sp.	83.9
							Pseudophycis bachus	13.73
							Algae	1.35
17 Oct.	930	65.1-120mm	43.64	79.54	0.39	18.17	Mysid sp.	78.50
							Pseudophycis bachus	18.70
							Algae	1.91
2 Dec.	900	0-120mm	20.18	34.89	48.35	12.81	Bivalves	30.41
							Dosinia subrosea	14.34
							Pseudophycis bachus	12.81
2 Dec.	1000	0-65mm	8.20	31.38	44.22	7.16	Bivalves	44.22
							Mysid sp.	21.95
							Amphipods	7.23
2 Dec.	1000	65.1-120mm	7.32	59.85	2.65	30.45	Pseudophycis bachus	30.45
							Mysid sp.	28.47
							O. catharus	15.14
7 March	930	0-65mm	24.52	66.67	15.87	1.74	Hymenosomatids	49.10
							Polychaetes	13.73
							Dosinia subrosea	10.75
7 March	930	65.1-120mm	17.04	28.22	43.72	15.05	Bivalves	35.61
							Teleosts	13.92
							Polychaetes	11.53

Table 24 Major food categories in the diet of O. catharus from samples collected at Brighton Beach through 1985-86.

Measurement	Autumn	Winter	Spring		Summer		Autumn
			usual	offshore	Trawl 1	Trawl 2	
Carapace width range (mm)	32.2-116	44-117.8	31.8-116.8	51.8-112.2	48.8-114.8	42.8-114	31.6-123
Mean carapace width (mm)	70.5	83.8	71.8	75.2	77.7	77	82.6
Number of crabs collected	78	87	66	33	72	62	143
Percent empty foreguts	32.1	80.5	9.1	45.5	48.6	35.5	51.7
Percent sediment per foregut	9.6	3.5	3.03	14.6	22.8	20.8	17.6
Mean foregut fullness (1-7)*	3.0	1.6	5.8	2.33	2.86	2.56	2.6
Mean flesh freshness (1-4)+	NA	NA	1.13	2.25	2.89	2.45	2.74
Number of prey items per crab	3.85	0.24	13.4	2.42	1.11	1.23	2.49
Number of taxa per crab	1.43	0.24	3.6	2.27	1.0	0.92	1.91

Table 25 Combined data for O. catharus collected from Brighton Beach. Calculations include crabs with empty foreguts. * scale represents foreguts: 1 = empty to 6 = full and 7 = distended; + scale represents: 1 = fresh flesh consumed within 1 hour of collection, 4 = food well digested 6-12 hours previous to collection.

feeding activity.. Flesh freshness values during Spring were low (1.73) supporting this hypothesis.

Tellina sp#1 (41.2 % IRI) and Zenobiana tubicola (37.3-48.5%) were the most important dietary species for crabs collected from Brighton Beach in autumn, 1985 (Table 24). Two months later during winter, Tellina, Z. tubicola, amphipods, hymenosomatids and algae were absent from crab diet, being replaced by decapods (49.95%), paddle crab cannibalism (30.15%) and bivalves (7.53%). For spring, Mysid sp.(78.5-83.9%) and the red cod Pseudophycis bachus (13.7-18.7%) were the most important food items in crab diet. Mysids dominated numerically with up to 56 individuals per stomach, while red cod were volumetrically weighted (27.1-33.6%), with 1-2 present per foregut. The dominance of mysids in crab diet continued on to summer (Fig.24), however, combined bivalves were the most important food in the diet of smaller crabs (44.2%) and P. bachus (30.45%) for larger crabs for the same period.

Paddle Crab Diet at Taylors Mistake

As insufficient crabs were available for analyses on a size class basis at Taylors Mistake during April and October all data for these months were combined. For autumn 1985, paddle crab diet was dominated by crabs (62.2%) followed by Mysid sp.(21.1%) and Tellina sp.#1 (10.1%)(Table 26). For spring, bivalves (72.2%) comprised the most important prey in crab diet followed by decapods (9.8%) and cumaceans (9.17%). The dominance of bivalves in small crab diet continued during summer when Tellina sp.#2 (76.9%) was 7 times more important than cumaceans and

Date	Time	Size Class	Gut Dry Weight per Crab (mg)	Percent Total IRI				
				Crustaceans	Bivalves	Fish	Three Most Important Taxa	
15 April	1100	0-120mm	4.99	85.92	12.08	0	*O. catharus*	62.23
							Mysid sp.	21.11
							Tellina sp#1	10.08
17 Oct.	1000	0-120mm	7.21	26.73	72.56	0.2	Bivalves	72.21
							Decapods	9.81
							Cumaceans	9.17
2 Dec.	1030	0-65mm	9.55	15.49	80.74	3.62	*Tellina* sp#2	76.9
							Cumaceans	8.93
							Hymenosomatids	4.28
2 Dec.	1030	65.1-120mm	10.57	6.87	83.29	8.0	*Tellina* sp#2	76.11
							Teleosts	8.0
							Dosinia subrosea	7.33
7 March	1000	0.65mm	3.46	57.96	15.99	3.51	Hymenosomatids	24.91
							Decapods	21.99
							Bivalves	15.99
7 March	1000	65.1-120mm	23.06	39.02	2.65	36.32	Decapods	34.77
							Pseudophycis bachus	26.56
							Pectinaridae	22.0

Table 26 Major taxonomic categories and food types present in the diet of *O. catharus* for samples collected at Taylors Mistake, 1985-86.

Measurement	Autumn 1985	Spring	Summer	Autumn 1986
Carapace width range (mm)	35-90.2	53-112	43-108	35-103
Mean carapace width (mm)	68	71.2	68.6	67.9
Number collected	14	36	111	43
% empty foreguts	50	30.6	49.5	46.5
% sediment per foregut	0.83	18.3	12.6	15.3
Foregut fullness (1-7)*	1.67	2.81	2.74	2.46
Flesh freshness (1-4)+	NA	1.64	2.84	2.67
Prey items per stomach	1.6	3.34	2.19	1.88
Prey categories per stomach	0.73	2.56	1.01	1.59

Table 27. Combined data for O. catharus collected from Taylors Mistake. Calculations inlcude crabs with empty foreguts. * scale represents foreguts; 1 = empty to 6 = full and 7 = distended; + scale represents :1 = fresh flesh consumed within 1 hour of collection, 4 = food well digested 6-12 hours previous to collection.

		Percentage Common Pairs			
		Little Akaloa		Brighton Beach	Taylors Mistake
Month	Size Class	Benthos	Epiben	Epibenthos	Epibenthos
June	0-65mm	27	47		
	65.1-120mm	38	40		
Sept	0-65mm	33	44		
	65.1-120mm	30	30		
Oct	0-65mm			55.6	
	65.1-120mm			50	
	0-120mm				25
Dec	0-65mm	40	53		
	0-120mm	33	44.4		
March	0-65mm			44	38
	65.1-120mm			43	50

Table 28. Percentage of food items recorded from benthic and epibenthic collections also present in the diet of O. catharus.

teleosts. Hymenosomatid crabs (24.9%) and other decapods (21.9%) were the most important prey of small crabs in autumn 1986, while large crab diet was dominated by decapods (34.8%), red cod and a pectinereid polychaete (22%).

Thirty to fifty percent of paddle crab foreguts collected from Taylors Mistake were empty (Table 27). Foregut fullness, flesh freshness, number of prey items and prey categories per stomach suggested, that the highest levels of feeding occurred during spring (October), however, the percent dry weight of food per foregut during summer (9.55–10.57%)(Table 27), surpassed spring values (7.21%). This was probably due to the greater percentage of the heavy bivalve shells present in foreguts of crabs collected in December.

RELATIONSHIPS BETWEEN CRAB DIET AND PREY AVAILABILITY

Diet overlap values, calculated using the Pianka (1973) equation, were rejected. The Pianka test compares the relative abundances of each diet pair and is unsuitable here as pairs were numerically different. This resulted in similarity values which increased as the number of pairs common to the diet and the fauna declined. The difficulties associated with sampling the heterogeneous and expansive marine benthos may be responsible for the large numerical differences encountered. Instead, a simple measure of the species common to crab diet and present in the environment were calculated (Table 28).

A total of 60–90% of species found in crab diet originated from the benthos or epibenthos (Table 28). At Little Akaloa, high overlap values, suggested that a greater proportion of crab

prey originated from the surface of the sediment. Overlap values at Brighton Beach suggested that crabs consumed even more prey from the benthos surface at this site than at Little Akaloa. At Taylors Mistake, however, low epibenthic overlap values supported dietary findings that crabs selected more prey here from within the benthos.

Combined data for paddle crab diet and faunal collections at each site suggest that the most abundant items in the diet were not the most common in the environment (Fig 23). Similarly, abundant items in the environment were not the most important items in crab diet.

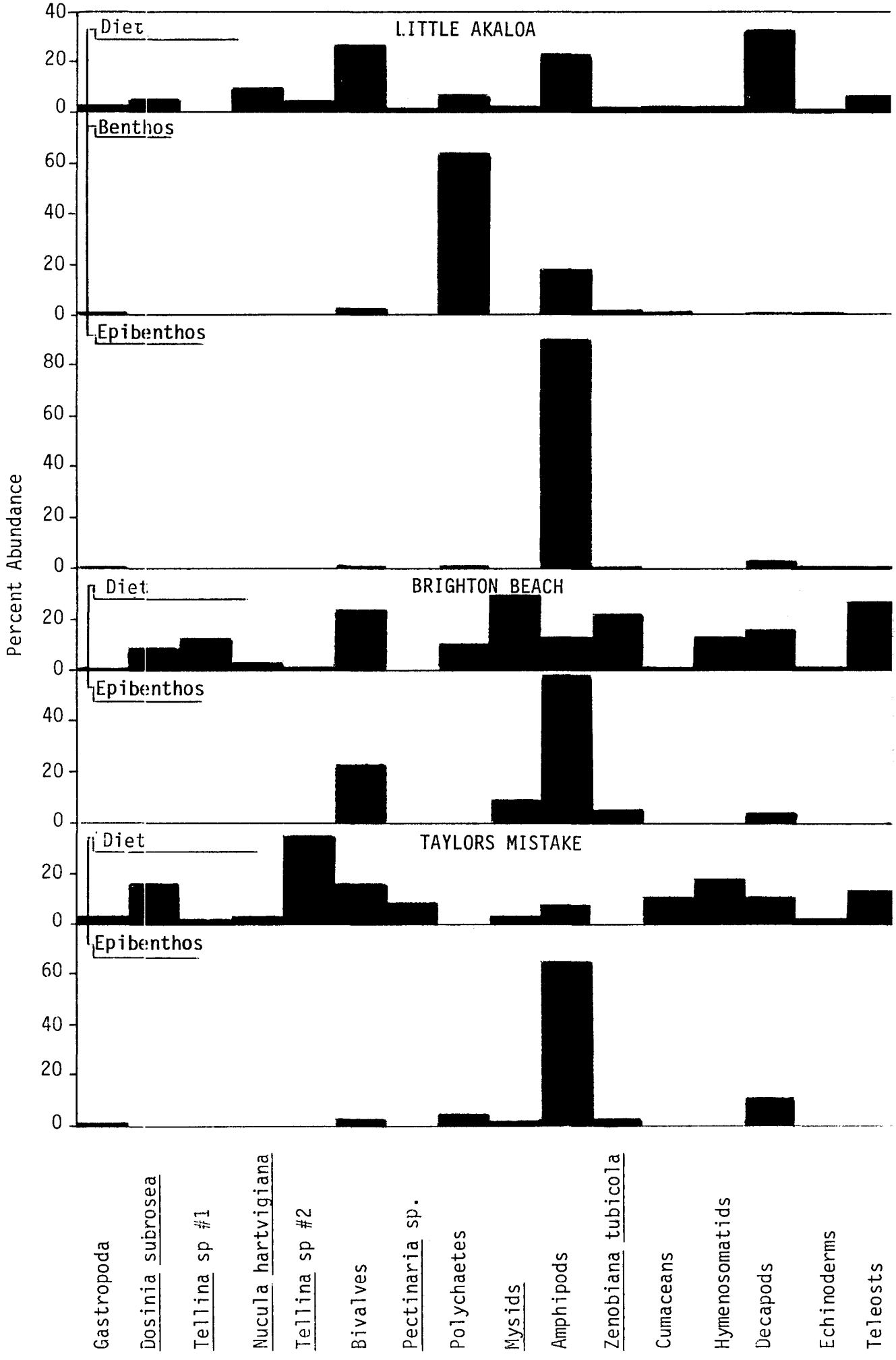


Fig 23. Diet of O. catharus, and benthic and epibenthic faunas found at the Banks Peninsula sample sites, 1985-86.

FACTORS AFFECTING THE DIET OF PADDLE CRABS

VARIATICN IN DIET WITH CRAB SIZE

The influence of predator size on paddle crab diet was determined by combining data for all seasons and sites (Fig.24). Small crabs from Little Akaloa consumed more amphipods, bivalves and mysids than larger crabs, where decapods, cannibalism and algae were important. Mysid sp. represented 25% more of the total IRI in small, compared with large crab diet at Brighton Beach (Fig.24). Bivalves and teleosts were more important in the diet of large crabs at Brighton Beach. The importance of teleosts in large, compared with small crab diet was the only significant difference at Taylors Mistake.

In general, both size groups of predator from all sites consumec similar prey. Differences were recorded, however, in the diet of each size class in the relative abundance, occurrence and volumetric composition of prey. Larger prey including decapods and teleosts were more predominant in large crab diet, while small crabs consumed smaller, softer bodied animals such as amphipods, mysids, cumaceans and isopods. Bivalves were present in the diet of both size classes of predator in similar proportions. Although cannibalism was greatest in larger crabs, it is uncertain whether crab carapace found in the foregut originated from live or recently moulted crabs. The food mastication process and the foregut size of small crabs made positive identification of paddle crabs in the diet difficult. Therefore, cannibalism could not be accurately assessed for either size of predator.

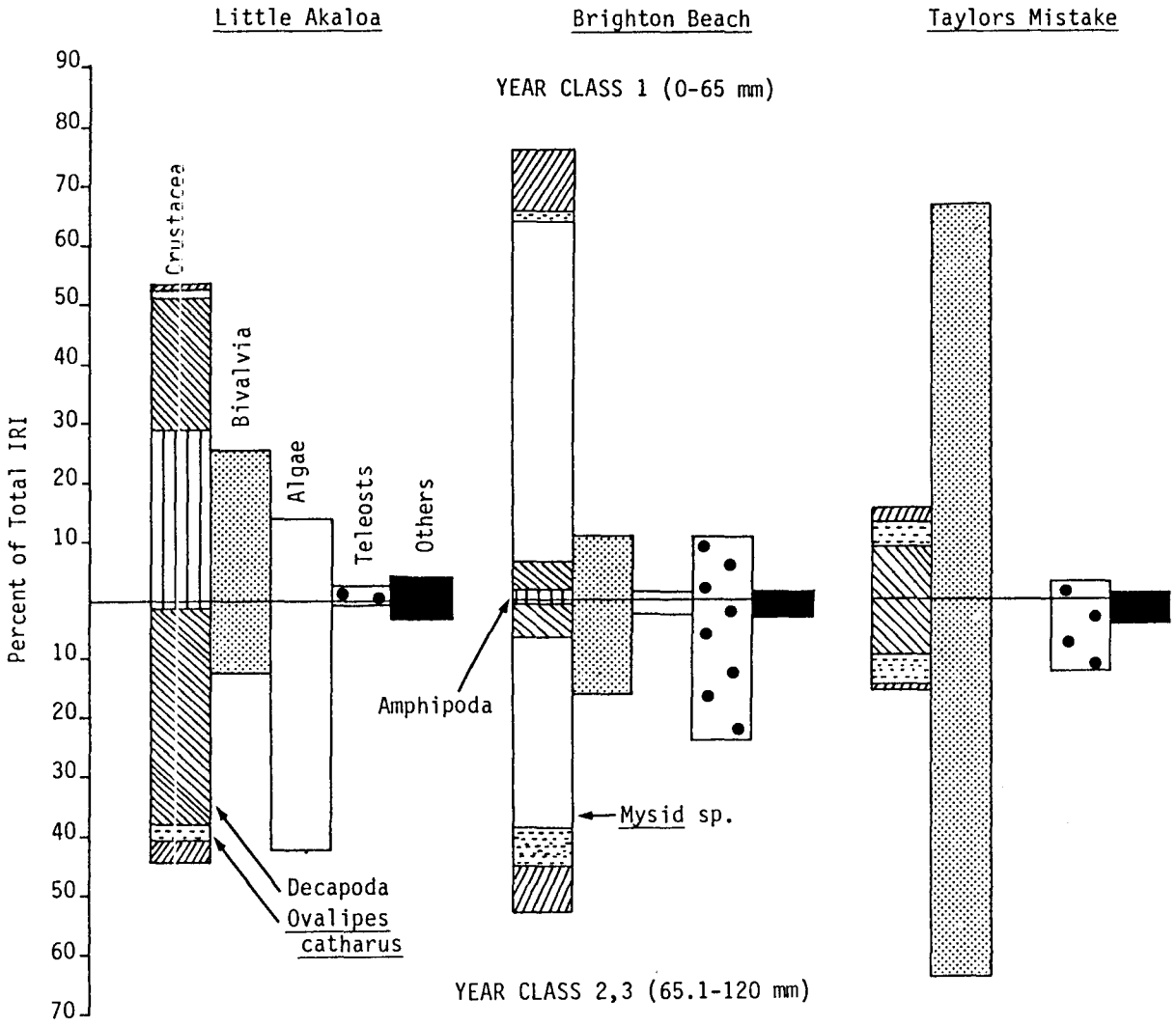


Fig 24. Relative composition of diet of 2 size classes of crabs collected at the 3 sample sites combined from all sample data. All prey items were grouped into 4 major categories: Crustacea (hatched bars), Bivalvia (stipled), Algae (open bars), Teleosts (dots) and others (filled bars). Bar lengths represent total percentage IRI for each prey category.

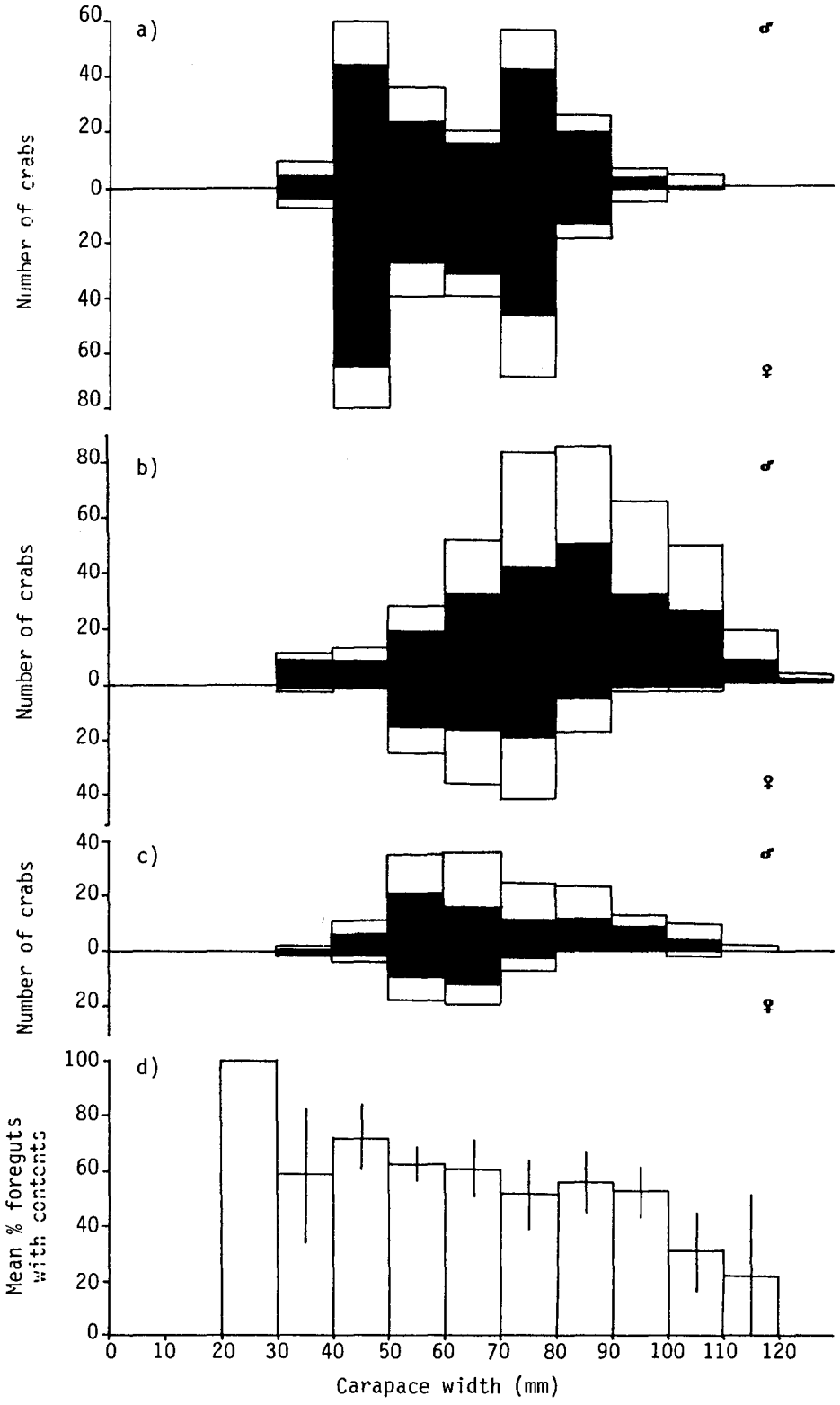


Fig 25. Size frequency distribution of all O. catharus collected 1985-86. Shaded areas represent proportion of total foreguts containing organic material: a) Little Akaloa (♂ 59.6%, ♀ 56.6%); b) Brighton Beach (♂ 57%, ♀ 56.7%); c) Taylors Mistake (♂ 39%, ♀ 42.2%); and d) Percentage of total foreguts collected with contents, relative to crab size for the combined sites for 1985-86. Error bars represent 95% confidence limits.

Mean percentage food contained in the foregut of crabs was calculated for twelve 10 mm size groups up to 120 mm carapace width for each site and for all sites combined (Fig 25d). The percentage of crab foreguts containing food declined with size to 21-30% for crabs larger than 100 mm CW.

DIEL CHANGES IN PADDLE CRAB DIET

The importance in crab diet of the four major prey categories (Crustacea, Bivalvia, Algae and "others") on a tidal and diel basis were calculated from combined samples from Little Akaloa (Fig 26). Dietary values represented feeding for the high tide previous to the collection: early morning for the period up to and including day break, and evening represented the afternoons foraging through to dusk.

Predation on crustaceans (51.3%) was highest during the daylight hours (0600-1200 h), while predation on bivalves (52.5%) was highest during the hours of darkness (0000-0600). Crustaceans were less important in crab diet at night (39.2%), while bivalve importance declined during daylight hours (26.8%)(Fig.26). This trend continued throughout the year when morning and afternoon collections were made, but was most pronounced in spring 1985.

Table 29 shows mean feeding activity values for combined samples from winter, spring and summer 1985 at Little Akaloa. Mean percent empty stomachs, number of prey items per crab stomach and gut fullness declined from morning to afternoon, suggesting a decline in the volume of food consumed during the daylight hours. Flesh freshness and the number of taxanomic

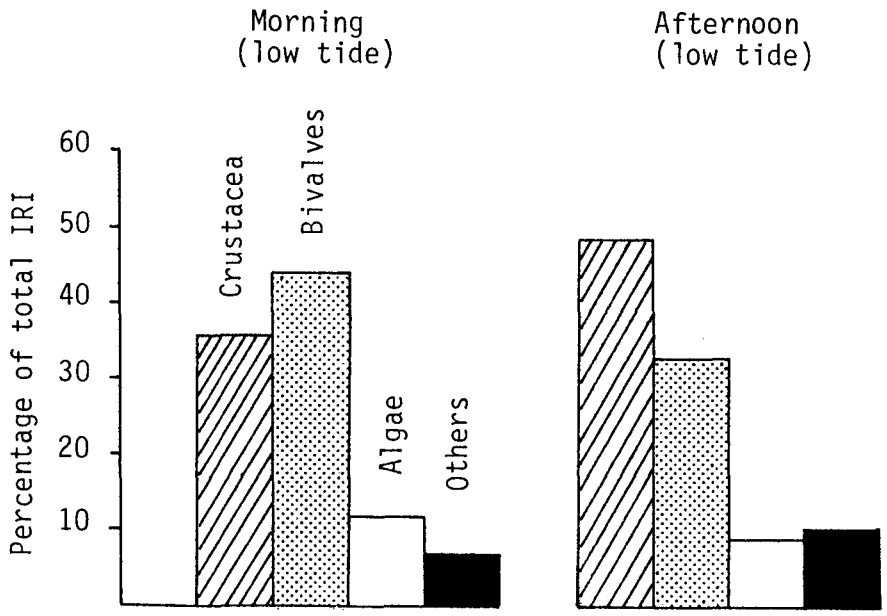


Fig 28. Diet changes for consecutive low tides, in the early morning and late afternoon at Little Akaloa. Values are mean percentage of total IRI for the 4 major food types: Crustacea (hatched bars), Bivalves (stippled bars), Algae (clear), and Others (shaded bars).

Variable	Morning	Afternoon
Percentage of foreguts empty	24.6 ± 2.8	30.75 ± 23.8
Mean foregut fullness (1-7)*	2.93 ± .12	2.81 ± .72
Mean flesh freshness (1-4)+	2.83 ± .38	2.74 ± .16
Number of prey items per crab	2.5 ± 1.1	1.89 ± 1.3
Number of prey taxa per crab	1.3 ± .31	1.35 ± .56

Table 29. Combined site and size class data for morning and afternoon collected crabs during the months of June, September and December at Little Akaloa. Values are represented with 95% confidence intervals.

categories per stomach, however, showed the opposite trend, suggesting that continued feeding occurred through the daylight high tide at a reduced level. These findings suggest that highest levels of feeding activity did not always occur in the early morning, nor were they seasonally consistent. During winter (June), highest levels of feeding were recorded during the daylight high tide.

VARIATION IN DIET WITH SEASON

The importance of the major prey categories in the diet of paddle crabs varied seasonally at each sample site (Fig.27) (Table 30). Crustaceans were important in the diet of paddle crabs during autumn and winter. Crustacean dominance was depressed in spring and was replaced by bivalves at Little Akaloa and Taylors Mistake during late spring and summer. In summer and autumn bivalves were important in crab diet at Brighton Beach, however, crustaceans consistently comprised the bulk of food eaten. Overall, seasonal changes in crab diet were characterised by consumption mainly of crustacean during the cooler months and a diet consisting of bivalves during the warmer months (Fig.27). These patterns may correspond with seasonal food availability.

VARIATION IN DIET WITH SEX

Female paddle crabs were numerically dominant at Little Akaloa, while males dominated at Brighton Beach and Taylors Mistake (Fig.25). The proportion of food in crab foreguts was similar for both sexes. The abundance and the type of prey occurring in the diet of each sex was similar (Fig.28). However,

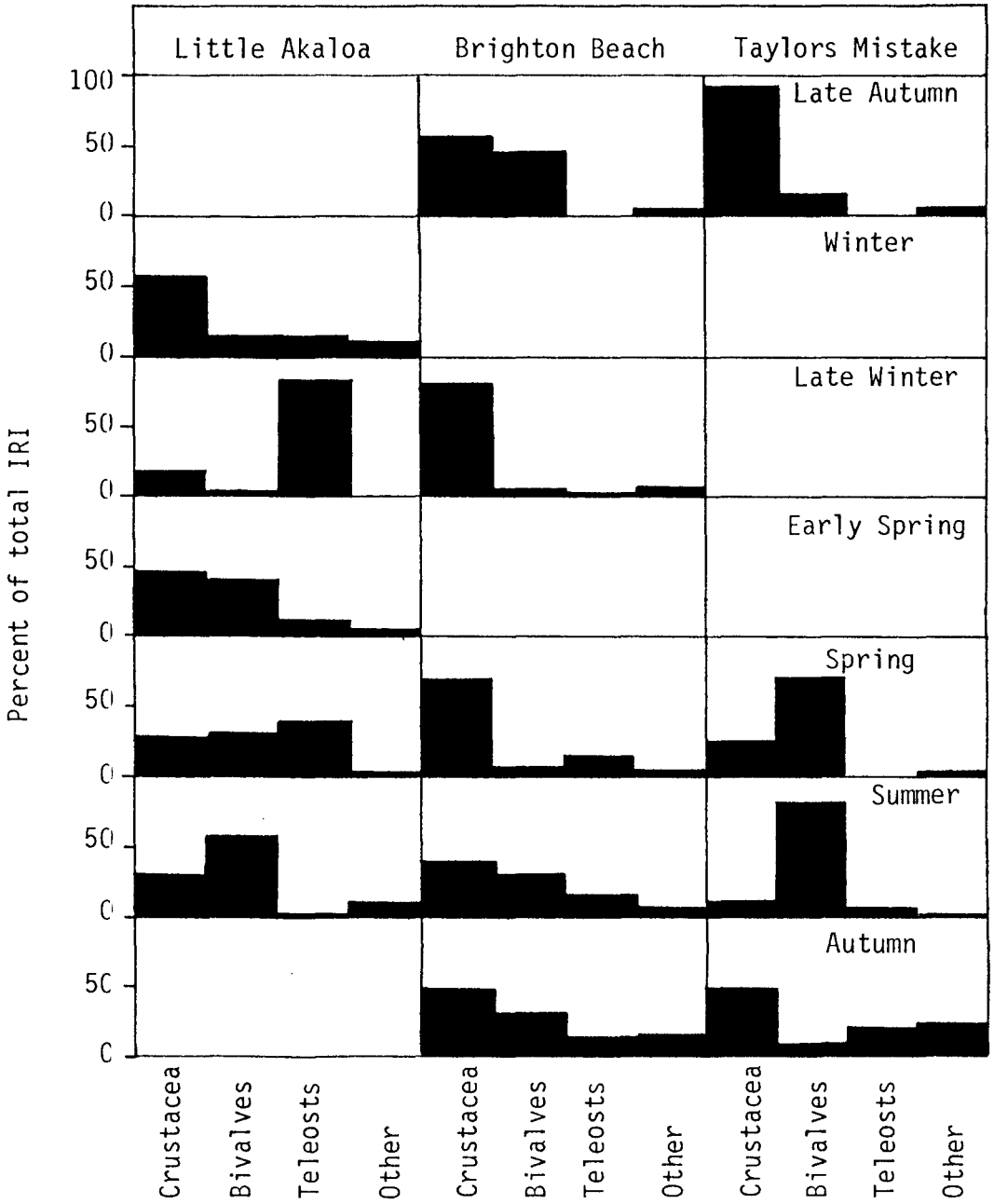


Fig 27. Relative composition of the diet of O. catharus throughout the year at Little Akaloa, Brighton Beach and Taylors Mistake. All prey sites are grouped into 4 major categories: Crustacea, Bivalva, Algae or Teleosts and others. Bar lengths represent total percentage IRI for each prey category.

Site	Season	Pairs	H value	P	Significance
Little Akaloa	Winter	16	7.57	.001	*
	Spring	7	0.15	.67	NS
	Summer	16	7.57	.006	*
Brighton Beach	Autumn	11	0.001	.435	NS
	Winter	6	5.39	.019	*
	Spring	9	2.0	.154	NS
	Summer	17	9.93	.002	*
	Autumn	14	8.12	.004	*
Taylors Mistake	Summer	10	0.41	.527	NS
	Autumn	13	0.02	.634	NS

Table 30. Kruskal-Wallis one-way ANOVA comparing diets of small (0-65mm) and large (65.1-120mm) O. catharus. *Significant difference, NS no significant difference.

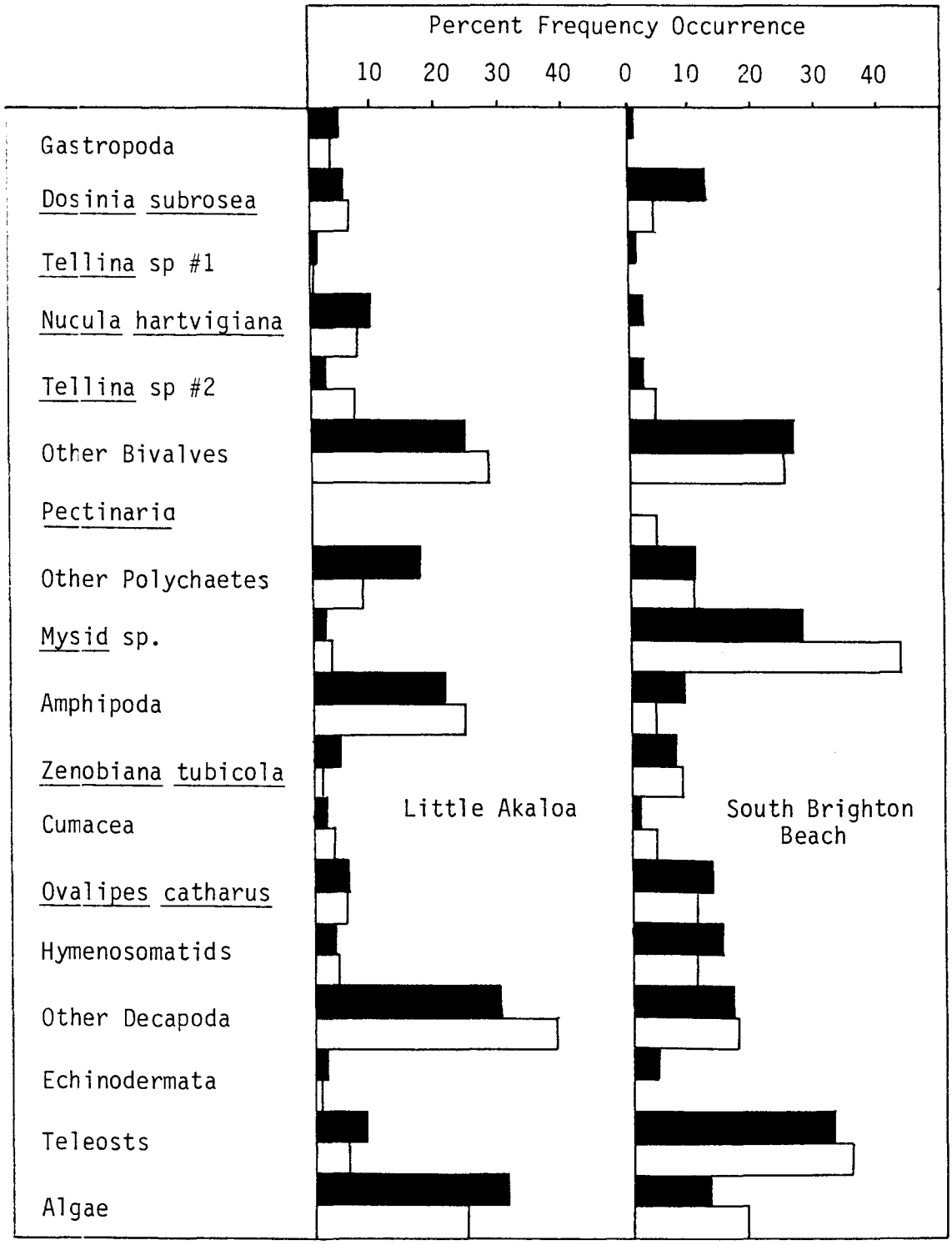


Figure 28. Percentage frequency occurrence of prey for male (shaded bars) and female (open bars) Ovalipes catharus of Little Akaloa and South Brighton Beach.

at Little Akaloa polychaetes were more important in the diet of male crabs (17%) than female crabs (8.2%). Female crabs at Brighton Beach consumed more mysids (43%) than male crabs (27%). Dietary differences recorded between paddle crab sexes are minor and are most likely due to sample variation.

EFFECTS OF OVIGEROUS STATE ON CRAB DIET

Insufficient ovigerous females were collected to compare their diet with that of non-egg bearing crabs. Three out of the four foreguts examined from ovigerous females contained food and were more than 25% full. These results suggest that female crabs continue feeding while carrying eggs.

VARIATION IN CRAB DIET WITH CARAPACE CONDITION

Paddle crab carapace condition was classified into six groups according to the moult stage. These groups were: a) post moult - shell extremely thin and soft; b) paper stage - carapace thin and firm; c) brittle stage - carapace thin, calcification beginning; d) hard shelled - carapace fully calcified; e) aged - carapace covered with growths and discoloured, chelae teeth broken or worn and; f) pre-moult - new shell well developed beneath the old carapace.

Feeding activity, represented by foregut fullness was measured for each moult condition. Variations due to site and season were minimised by using a total of 277 crabs collected from Brighton Beach in summer and autumn (2 December, 1985 and 6 March, 1986). Feeding activity measurements were restricted to crabs greater than 50 mm, as moult stage could not be reliably

assessed for small crabs due to their high moult frequency.

Forty-eight percent of foreguts from pre-moult and post-moult crabs were empty, while 52% of foreguts contained less than 15% of sediment or food (Fig.29). This suggests that like the other brachyuran crabs (Waterman, 1960) including Carcinus maenas (Ropes, 1968; Elner, 1980) Callinectes arcuatus and C. toxotes (Paul, 1981), O. catharus ceases feeding prior to and after ecdysis. In recently moulted sand crabs, Portunus pelagicus (Williams, 1982) the gastric mill was filled with small pieces of calcarious material actively selected from the substratum. Few soft shelled O. catharus contained food items or sediment in the foregut (Fig.30). Prey items consumed by crabs at all moult stages were similar. Crabs with recently hardened shells, however, consumed more bivalves than pre-moult or aged crabs which consumed a greater proportion of decapods.

The frequency with which prey items occurred in crab diet increased as the carapace hardened (Fig.30) suggesting, that increased calcification of the chelae and mouthparts allowed crabs to attack and open prey with greater success. The proportion of crabs in the hardened stage exceeded the number of soft shelled individuals, therefore, predation by hard shelled crabs would have a greater impact on prey populations.

Samples taken during December and March, 1985-86, showed that 16% of paddle crabs were in a pre-moult or post-moult condition, 37% were hardening (stages 2 and 3), and 47% were fully hardened (stages 4 and 5). The proportions of crabs in each stage was expected to vary seasonally. Therefore, predation pressure and rates of cannibalism would also be expected to vary

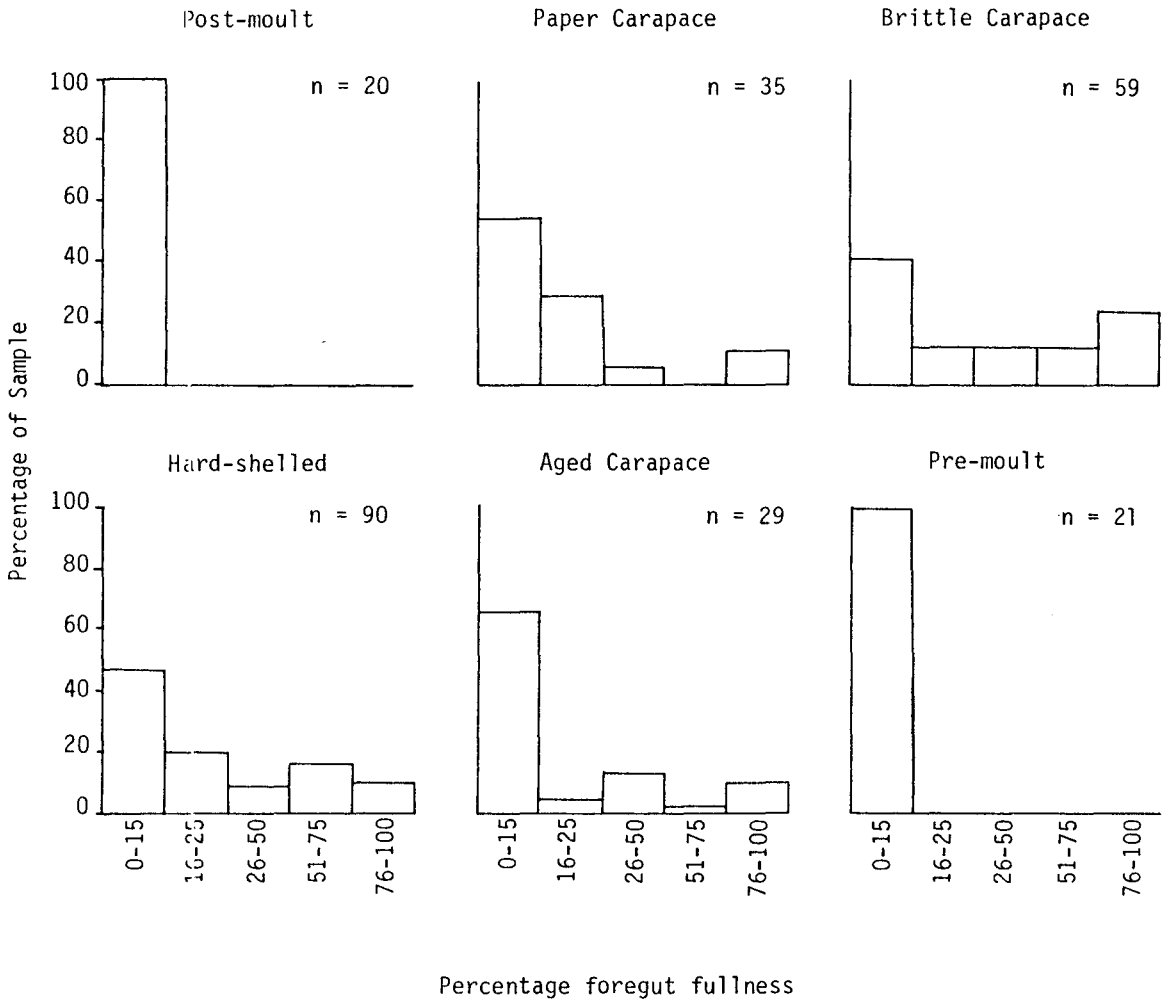
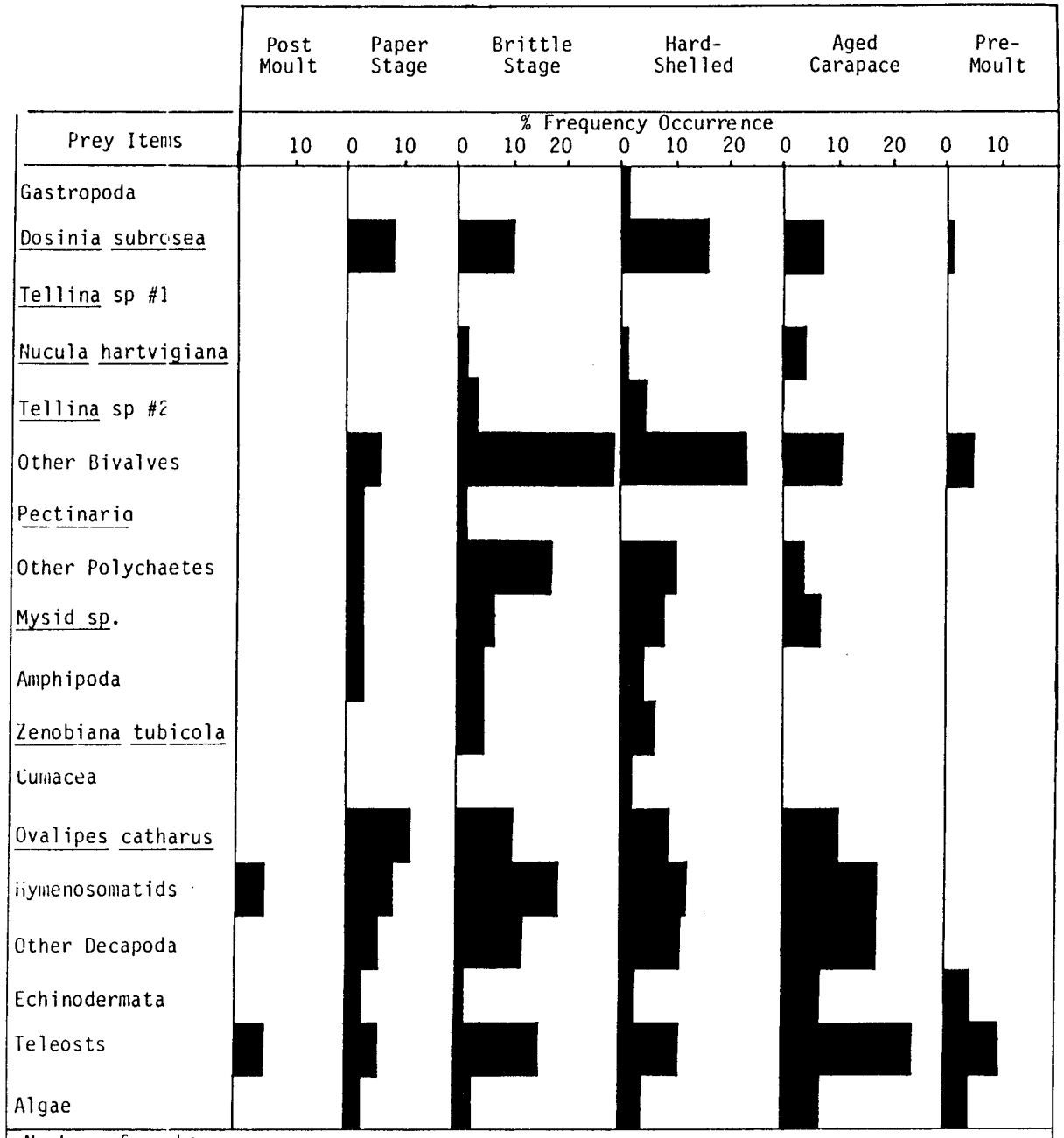


Fig 29. The percentage of O. catharus foreguts falling into 5 fullness categories (0-15, 16-25, 26-50, 51-75 and 76-100%) relative to moult stage. Samples collected from Brighton Beach 2 December 1985 and 6 March 1986.



	Post Moult	Paper Stage	Brittle Stage	Hard-Shelled	Aged Carapace	Pre-Moult
Number of crabs per group	20	35	59	90	29	24
Number with contents	2	18	42	66	15	6
Percentage with contents	10%	51.4%	71.2%	66.7%	51.7%	28.6%

Fig 30. Frequency occurrence of food items relative to carapace condition at South Brighton Beach 2 December 1985 and 6 March 1986.

seasonally.

VARIATION IN DIET WITH TRAWL AND TRAWL LOCATION

The importance of the four major food categories in large crab diet were calculated for collections from Brighton Beach during two replicate trawls (Fig.31). Collections were restricted to a 1 km area within 1 km of the surf zone. Comparison of diets of crabs from each replicate trawl indicated that crustaceans, teleosts and "others" remained at similar levels of importance in the diet. IRI values for bivalves, however, declined from 48.8% in trawl 1 to 2.6% in the 2nd trawl (Fig 31). Results suggest that bivalve populations at Brighton Beach are irregularly distributed. Crustaceans and teleosts appear to be more evenly distributed within the area sampled.

Comparison of diets of larger crabs collected from the inshore site and a site 2-3 km offshore on 17 October 1985 showed that bivalves were again consumed by crabs in different proportions (Fig.32). Crustaceans were the most important component in the diet of crabs at both sites. Crustaceans were, however, more important for crabs from the inshore site due to the near absence of bivalves (0.38%). Bivalves composed 21% (IRI) at the offshore site. These results support the findings that bivalves are irregularly distributed within the benthos, resulting in their variable importance in crab diet with location.

EFFECT OF TEMPERATURE ON CRAB DIET

The percent crab foreguts containing food were plotted

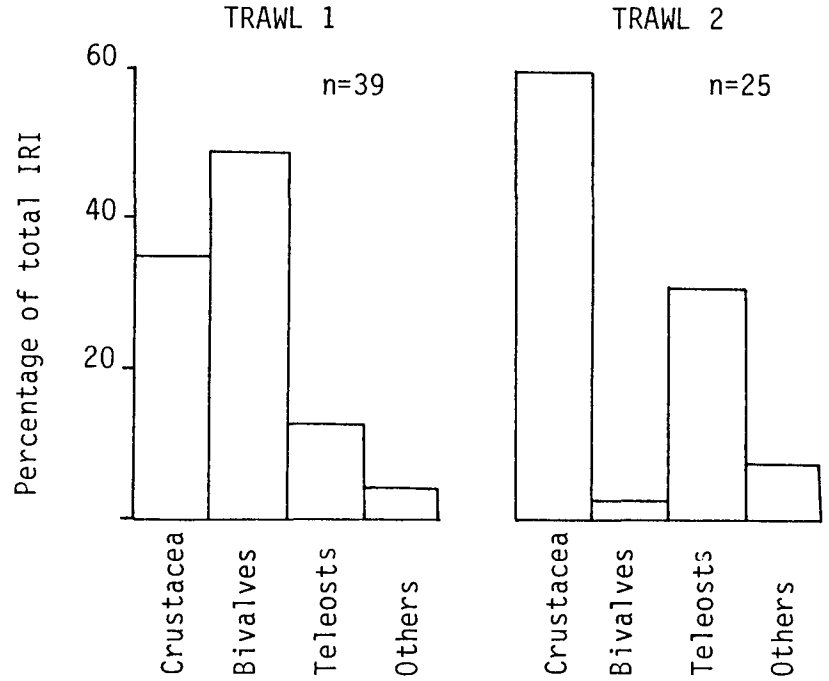


Fig 31. Relative importance of the 4 major food categories from 2 large crab samples taken 2 December at Brighton Beach. Trawls were taken within a 1 km² area of a surf zone.

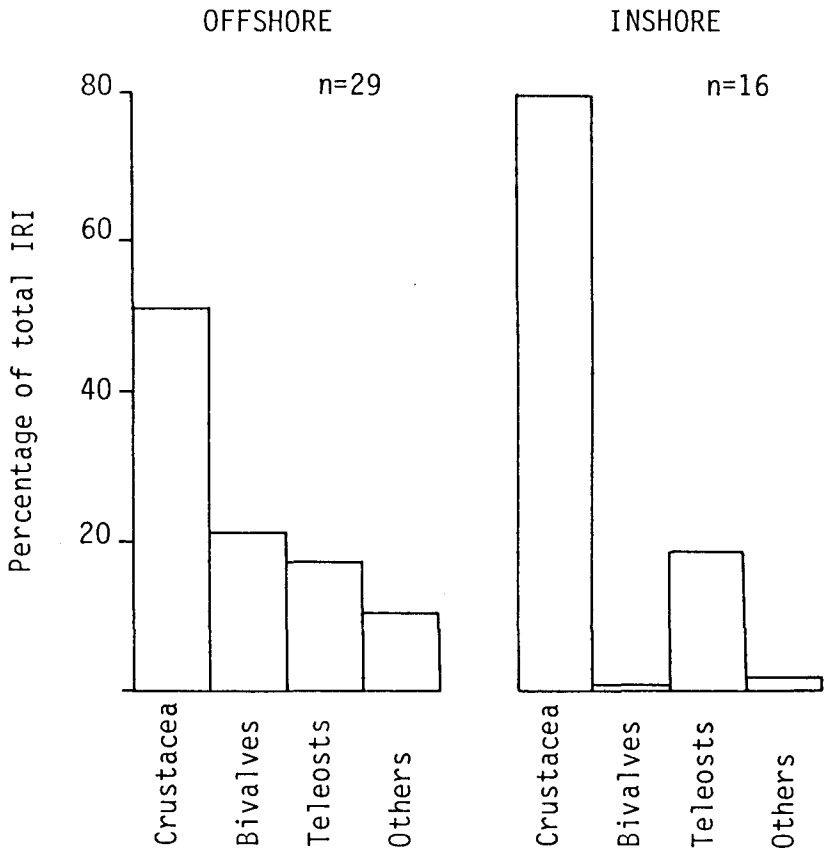


Fig 32. Relative importance of the 4 major food categories in the diet of large O. catharus from an inshore trawl, take with 1 km of a surf zone and an offshore trawl, 2-3 km from the surf zone. Samples taken 17 October 1985 at Brighton Beach.

against temperature at Little Akaloa and for combined samples from Brighton Beach and Taylors Mistake (Fig.33). Low foregut fullness values were expected to represent suppressed levels of foraging activity in the population, possibly related to changes in temperature.

Reduced environmental temperatures at Little Akaloa in autumn and early winter corresponded with a decline in the proportion of crabs feeding (40.5 %). This result was more pronounced at the combined Brighton Beach and Taylors Mistake sites where only 19.2% of crabs had recently fed. As temperature increased from October onwards, the number of crabs with food in their foreguts increased (Fig.33). Feeding activity in half the crabs collected, however, resumed prior to significant temperature increases. This suggests that increased temperatures alone may not be the only factor involved in increasing feeding activity. Other factors may include temperature acclimation, increased hunger levels, increased prey availability and lunar cycles.

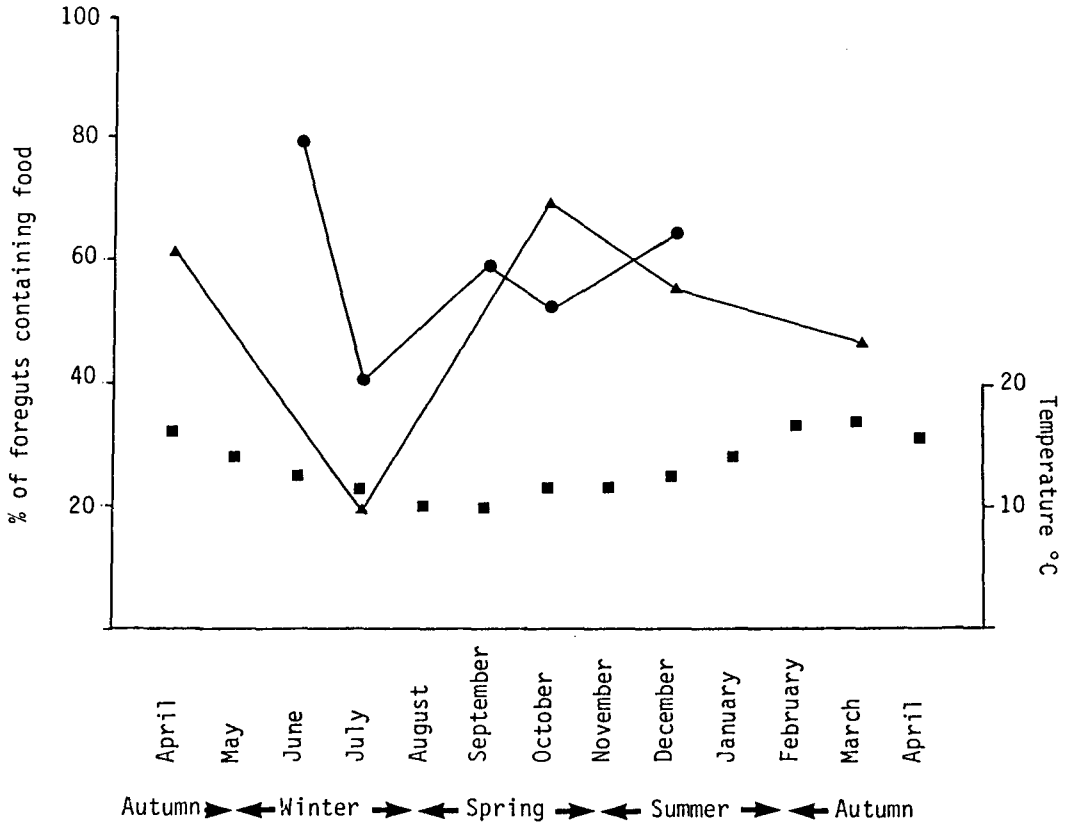


Fig 33. Percentage of crabs containing food in combined samples from Brighton Beach and Taylors Mistake (triangles) and Little Akaloa (circles) relative to water temperature (closed squares) throughout 1985-86.

DISCUSSION

Natural diet and Predatory Behaviour

In the past portunid crabs have been regarded as opportunistic generalist predators (Ropes, 1968; Elner, 1981; Williams, 1981; Stevens et al., 1982; Haefner, 1985). A conclusion based mainly on the variety of food items included in crab diets. This present study confirms this general statement providing for the first time, information about the availability of potential prey.

For Ovalipes catharus collected in the Canterbury area, the diet varied both with location and season. Paddle crab diet comprised mainly of mobile epibenthic crustaceans, particularly isopods, mysids, decapods and amphipods, and to a lesser extent on bivalves and fish. The presence of small whole fish in paddle crab diet suggested that crabs were capable of capturing live individuals.Stead (1983) observed Ovalipes catharus attacking small flat fish on the bottom and mullet and other small fish near the surface. Plant material was present in crab diet at most sites and during most seasons. Whether plant material can be digested by O. catharus is not known. Yokoe and Yasumasu (1964), recorded cellulase activity originating from heptopancreatic and gastric extracts from 18 species of crustacea, five of which were decapods. These findings suggest that O. catharus may selectively feed on algae gaining sustenance in the form of laminarin (a polysaccharide sugar)(Chapman and Chapman, 1980) during periods of low organic food availability. Choy (1986) found that algae was the single most important item in the diet of large Liocarcinus puber, while

in the laboratory these crabs preferred organic material. Similarly, for combined samples at Little Akaloa, algae was the single most important item for large O. catharus. At the other sites p'ants formed a small part of crab diet and was probably consumed coincidentally with other food items. Crabs also consumed bryozoans, hydrozoans and sediment, eaten coincidentaly by crabs feeding on organisms living on or within these items.

Natural diet studies on the portunid crabs Carcinus maenas (Ropes, 1968; Elner, 1981), Calinectes arculatus and C. toxotes (Paul, 1981), Cancer magister (Gotshall, 1977; Feder and Paul, 1980), Portunus pelagicus (Williams, 1981), Scylla serrata (Hill, 1979) and Ovalipes stephensoni (Haefner, 1985) found that bivalves dominated crab diet. Stevens et al. (1982) found that fish were most important in the diet of Cancer magister in Washington State, while Butler (1954) found the diet of C. magister at Hecate Strait British Columbia was primarily composed of crustaceans. Kung (1973) found the diet of O. catharus was dominated by crustaceans at Paremata Beach, Wellington. Wear and Haddon (in press), found that crustaceans dominated the diet of O. catharus at 5 sites, while bivalves were dominant at 6 sites around northern New Zealand. In this present study, paddle crab diet was dominated by crustaceans at two sites, while bivalves were the most important prey category at a third site. Differences in crab diet with location were probably a reflection of prey availability.

Seasonal differences in prey availability at each site were also reflected in paddle crab diet throughout the year. Seasonal dominance of bivalves in crab diet at Little Akaloa and mysids

and teleosts at Brighton Beach during spring and summer coincided with highest prey densities. The decline of bivalves in crab diet during late autumn and winter was probably due to bivalve depletion combined with their ability to burrow deeper with increasing size (Virstein, 1979; Blundon and Kennedy, 1982b; Haddon and Wear, in press).

Prey availability influences prey selection by predators (Virstein, 1977; Hughes, 1979; Hughes and Seed, 1981; Jubb et al., 1983; Pyke, 1984; Scrimgeour, in press). Paul (1981) suggested that the variation in Callinectes arculatus and C. toxotes diet was in response to prey availability. Most dietary studies have regarded portunid crabs as opportunists, consuming prey according to their relative abundance. However, little information exists concerning prey availability. From the prey surveyed in this study it was shown that paddle crabs ate the majority of prey present in an area. However, prey selection was not always directly related to abundance. Reports by Feder and Paul (1980), Allbright and Bouthillette (1982) and Stevens et al. (1982) have suggested that crabs may be selecting particular prey in preference to equally abundant items. Present studies on Ovalipes catharus suggested that abundance of prey alone did not determine prey selection. Amphipods and polychaetes dominated faunal collections, but were never consumed by crabs in similar proportions. The diet of paddle crabs was modified seasonally to take advantage of a temporary food source although the food previously consumed was still available. Although many aspects of feeding behaviour of portunid crabs have been investigated in the laboratory (Caine, 1974; Elner, 1978; Brown et al., 1979; Hughes,

1979; Heller, 1980; Seed, 1981; Jubb et al., 1983; Pyke, 1984; DuPreez, 1984; Rheinalt and Hughes, 1985; Skilleter and Anderson, 1986), such modification of feeding behaviour from field studies has not been found previously.

The feeding activity of paddle crabs varied throughout the day. Crabs collected in the early morning had more undigested whole food items in their foreguts than midday and evening collected crabs. This suggests that O. catharus feeds mainly during the night. Foreguts from crabs collected during the day, however, did include some freshly eaten material, suggesting some feeding activity. At night, during periods of increased foraging activity, few crabs could be captured in trawls. Day observations made using SCUBA revealed that crabs remained inactive, buried in the sand with only their eyes and antennules visible. This period corresponded with diets consisting mainly of mobile crustaceans and fish suggesting that paddle crabs may be ambushing these prey from their temporary day time burrows. In contrast, during the night, crabs are actively moving about and the diet consists mainly of bivalves.

The presence of large quantities of calcarious material in the foreguts of recently moulted crabs has been well documented (Knudsen, 1959; Ropes, 1968; Paul, 1981; Williams, 1982; Choy, 1986). This material is thought necessary for the formation of a new crab exoskeleton. The foreguts from paddle crabs before and immediately after ecdysis did not contain shell or carapace fragments. Heavy mud and silt load in the Pegasus Bay region

(Campbell, 1974) quickly buries calcarious objects required by crabs following moulting. Recently moulted paddle crabs do not feed and therefore, cannot obtain calcium during this period by feeding. Incorporation of crustacean prey prior to moulting may overcome temporary shortages of calcium in the post-moult condition. Bivalves are important in the diets of hardening crabs, supplying calcium required for further hardening of the carapace.

Cannibalism in portunid crabs including O. catharus has been well documented (Ropes, 1968; Gotshall, 1977; Paul, 1981; Stevens et al., 1982; Choy, 1986; Wear and Haddon, in press). This present study suggests that cannibalism in O. catharus increased during periods of increased crab abundance, moulting during winter and spring, megalopa settlement and growth of early instars. Cannibalism was most frequent in large paddle crabs, probably due to their larger chelipeds and greater mechanical advantage.

Predator Size and Feeding Mechanics

In many other studies (Ropes, 1968; Paul, 1981; Stevens et al., 1982; Choy, 1986) the diet of O. catharus was related to crab size. With increased crab size, smaller soft bodied prey such as amphipods and mysids declined in the diet, replaced by larger prey such as teleosts and decapods. These changes may be related to increased mechanical advantage of the chelipeds (Schaefer, 1970; Elner, 1979, 1981; Brown et al., 1979; Boulding, 1982).

The chelipeds of O. catharus are heteromorphic,

heterodontic, polyfunctional limbs, each specialized for various prey handling functions. As Ovalipes catharus grows the chelipeds retain their fine dactyli and propi (Davidson and Marsden, in press) allowing even the largest crabs extreme dexterity. Cheliped size was probably responsible for determining which prey were eaten by crabs. In the field, very small and mobile prey such as amphipods were eaten more often by smaller crabs. Results suggest that in O. catharus, chelae size and mechanical advantage may be underestimated as a factor influencing prey selection, particularly for very small prey. The advantage of slender, dexterous and polyfunctional chelipeds is that a wide range of prey types and prey sizes can be handled effectively by all sizes of crab. This contrasts with large shore crabs Carcinus maenas, which dropped or mishandled very small prey items (Hughes and Seed, 1981). The ability to successfully attack a wide range of prey types and sizes allows O. catharus to take advantage of seasonally abundant prey types.

The Impact of Paddle Crab Predation

Predation by crabs influences prey communities, particularly on marine soft bottoms and rocky shores (Ebling et al., 1964; Virstein, 1977; 1979; Holland et al., 1980; Blundon and Kennedy, 1982b; Boulding, 1984; Chilton, 1984). Comparisons of the relative abundance of prey items available in the environment with those eaten by Ovalipes catharus indicates how the predator may influence prey community structure and composition.

Faunal collections from Canterbury crab collection sites were dominated by benthic polychaetes and epibenthic amphipods.

Virstein (1977; 1979) characterised two general types of benthic organism based on their living habit and their response to predation. The first group were generally tough tube dwellers, or deep in the sediment animals. In Canterbury, these species included the burrowing and tube dwelling polychaetes Orbina papillosa, Maldanidae sp. and Heteromastides filiformis, and the burrowing amphipods Phoxocephalid spp. Polychaetes represented up to 82.2% of organisms in the benthos, however, they were not important in paddle crab diet. In the laboratory, paddle crabs eagerly consumed polychaetes when encountered (authors pers. obs.), therefore, it was concluded that polychaetes in field conditions escape predation. Peak predation on bivalves by paddle crabs coincided with peak abundance of predominantly small individuals. Predation levels declined as bivalves grow to adult size. Blundon and Kennedy (1982b), found that predation on Mya arenaria by Callinectes sapidus was less effective on clams that burrowed below 10 cm depth. Haddon and Wear (in press), found that predation on bivalves by paddle crabs declined in a linear fashion as bivalves burrowed deeper within the sediment. Six out of the nine bivalve species recorded in benthic samples burrow deep within the sediment as adults (eg. Panopea zelandica, 450 mm depth; Tellina liliana, 200 mm depth), thereby escaping predation by paddle crabs.

Fast moving, small epibenthic organisms were rare in the paddle crabs diet. The amphipods Allorchestes sp. and Atylus taupo were not important in large crab diet. Small crabs, however, consumed significant numbers of amphipods. This suggests that amphipods become a more difficult prey item to

capture as crabs became larger.

Virstein's second category of benthic organisms were those vulnerable to crab predation, living very close to the sediment surface. In Canterbury, such species were uncommon or found only sporadically in the environment. Decapods, bivalves, mysids and teleosts were, however, common in the diet of New Zealand paddle crabs. This study supports Virstein's findings that certain communities are able to withstand predation pressure by crabs. Laboratory experiments using O. catharus, suggested that low prey abundance (Davidson, 1986) or very high prey abundance (Haddon and Wear, in press) may afford a refuge from predation. In the environment, species depleted by crab predation would be encountered seldom by paddle crabs. Low predation levels would allow prey populations to reach high densities. Many prey species appear in high densities for short periods, thereby gaining density refuge during these periods.

The ability of prey species to gain refuge from predation, ensures that these populations are maintained. The adult reproductive success of species such as Tellina liliana, an important paddle crab prey as small individuals, is neccessary for a continued food resource for crabs and future bivalve populations. Over exploitation of adult bivalves by man may be more important factor leading to the depletion of bivalve stocks than paddle crab predation.

SUMMARY

Epibenthic and benthic invertebrates and the portunid crab Ovalipes catharus were collected seasonally from three sites around Banks Peninsula, Canterbury from 15 April 1985 to 12 March 1986. Composition and abundance of the fauna was compared with the natural diet of crabs, analysed using the Index of Relative Importance (IRI). Amphipods were the most important group in the epibenthos (64.5-95.9%), while polychaetes dominated the benthos (53.9-85.2). These items were not important in the diet of crabs. Prey items important in paddle crab diet were not abundant in faunal collections. Results suggest that O. catharus selectively forages. However, this was influenced by prey availability and varied with location and season. Epibenthic crustaceans were the most important food in the diet of paddle crabs from Brighton Beach and Little Akaloa while bivalves were important in crabs from Taylors Mistake. Teleosts formed the next most common prey in the diet of paddle crabs, while algae was important in the diet of large crabs from Little Akaloa. The importance of algae in the diet of paddle crabs during winter periods when numbers of benthic animals were low, suggested that crabs may gain some nutrients from plant material. The diet of Ovalipes catharus was affected by moulting, season, time of day, temperature and size of crab. Paddle crabs ceased feeding prior to moulting and following ecdysis when chelipeds and mouthparts were in a soft stage. Diel dietary studies suggested that crabs feed mostly during the hours of darkness, primarily on bivalves. Feeding during the day also occurred, primarily on crustaceans.

Crab size and the mechanical advantage of the chelipeds influenced the diet. Larger, calcified prey items were more important in the diet of large crabs. Smaller soft bodied animals were eaten more often by smaller paddle crabs. Reduced temperatures during winter corresponded with depressed feeding levels. However, feeding resumed prior to significant increases in temperature.

The amount of flesh remaining in the foregut of paddle crabs declined to 50% 1.5 h after feeding. All flesh was absent from the foregut 12 h after consumption. Ninety-nine percent of ingested shell was regurgitated 12 h after feeding. This dietary study, combining faunal survey techniques provides evidence that paddle crabs are selective foragers, taking advantage of particular, locally abundant prey. In this way, large numbers of paddle crabs are maintained in local waters.

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APPENDIX 1

THE RELIABILITY OF THE INDEX OF RELATIVE IMPORTANCE AND THE AFFECT OF SAMPLE SIZE AND FOREGUT FULLNESS

INTRODUCTION

The reliability of the diet analysis technique determines the credibility of any study of feeding habits. The particular method used is therefore an important consideration before undertaking lengthy analysis. Existing dietary information on portunid crabs (Hyslop, 1980; Elner, 1981; Paul, 1981; Williams, 1981; Choy, 1986) suggests that points, volumetric composition and frecuency occurrence methods yield similar results. No information, however, is available on how the Index of Relative Importance (IRI) compares with these methods as a measure of dietary importance. In this study of the natural diet of a decapod crustacean Ovalipes catharus the accuracy of a modified version of IRI (Pinkas et al., 1971) was compared using numerical, volumetric and frequency methods.

The number of crabs analysed determines the number of prey items recorded and the relative importance of each item in the diet (Williams, 1981). The number of crabs and the foregut fullness required to give a true indication of the natural diet were also calculated.

MATERIALS AND METHODS

Paddle crabs (35-120 mm carapace width) used for comparisons of dietary analyses methods were collected from Brighton Beach,

Canterbury during July, October, December and March 1985-1986. Crabs with empty foreguts were excluded. Crab foreguts were examined in no particular order and the data combined and compared using numerical composition, volumetric composition, frequency occurrence and Index of Relative Importance (IRI) methods. Gravimetric composition in the IRI equation (Pinkas et al., 1971) was replaced by volumetric composition due to the masticated state of the food in crab foreguts. The influence of sample size and foregut fullness were also examined using combined Brighton Beach samples.

RESULTS

Foregut Fullness and Sample Size

Figure 34a shows that the number of prey items recorded increased with foregut fullness (n=304). At 75% fullness, the number of prey items per crab recorded a maximun (2.6). The number of prey items recorded in the diet of paddle crabs increased as the number of foreguts examined increased (Fig.34b). Half the total number of prey items eaten by crabs were recorded after approximately six foreguts were examined, while 75% of all prey were recorded after 18 foreguts were analysed.

The minimum number of foreguts required to establish the important species in the diet of paddle crabs varied with sample date (Table 31). The most important taxa were recognised by between 4 and 11 foreguts, representing between 16-76.6% of the total sample size collected. These values may not, however, represent a stabilization of dietary importance, especially when

Table 31. Number of paddle crab foreguts required to determine the dominant prey category in the diet.

Date	Trial	n	Dominant Prey	Frequency Occurrence	no. Foreguts Required	%
July	1	17	Decapoda	47.06	12	70.6
October	1	58	Mysids	90.0	10	17.2
October	2	16	Bivalves	31.0	6	18.8
December	1	39	Bivalves	32.43	10	25.6
December	2	14	Bivalves	32.86	7	50.0
December	3	25	Teleosts	24.0	4	16.0
March	1	7	Ovalipes	28.6	4	57.0
March	2	62	Bivalves	37.09	11	17.0

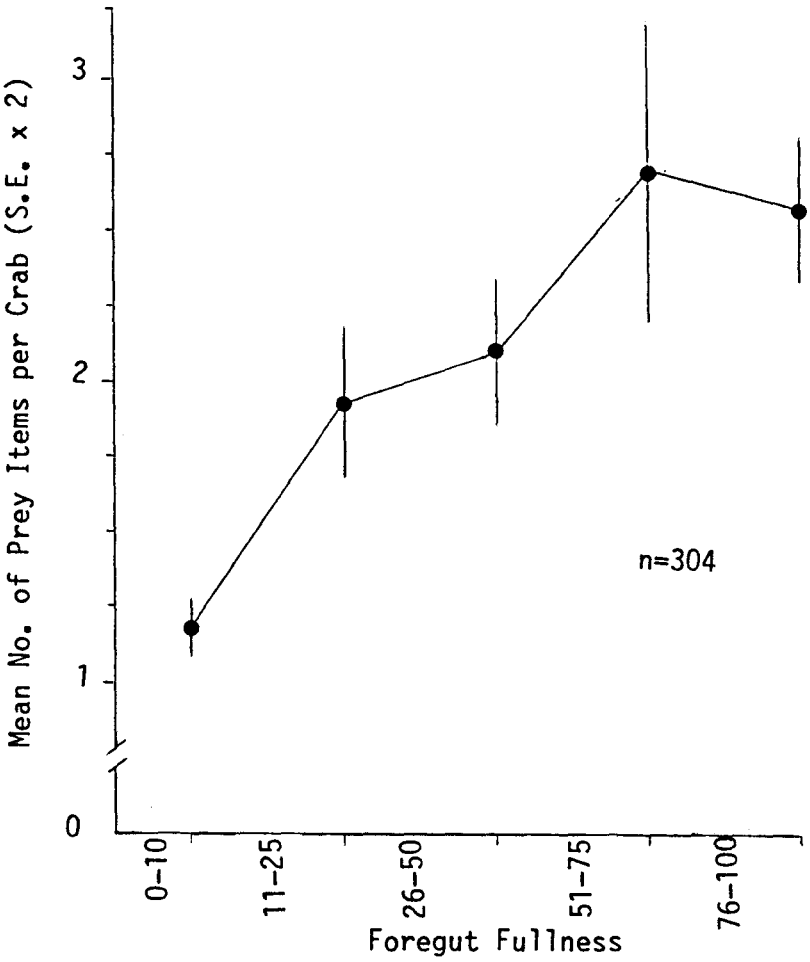

Fig. 34a. Mean number of prey items per foregut versus foregut fullness for O. catharus. Error bars represent 95% confidence intervals.

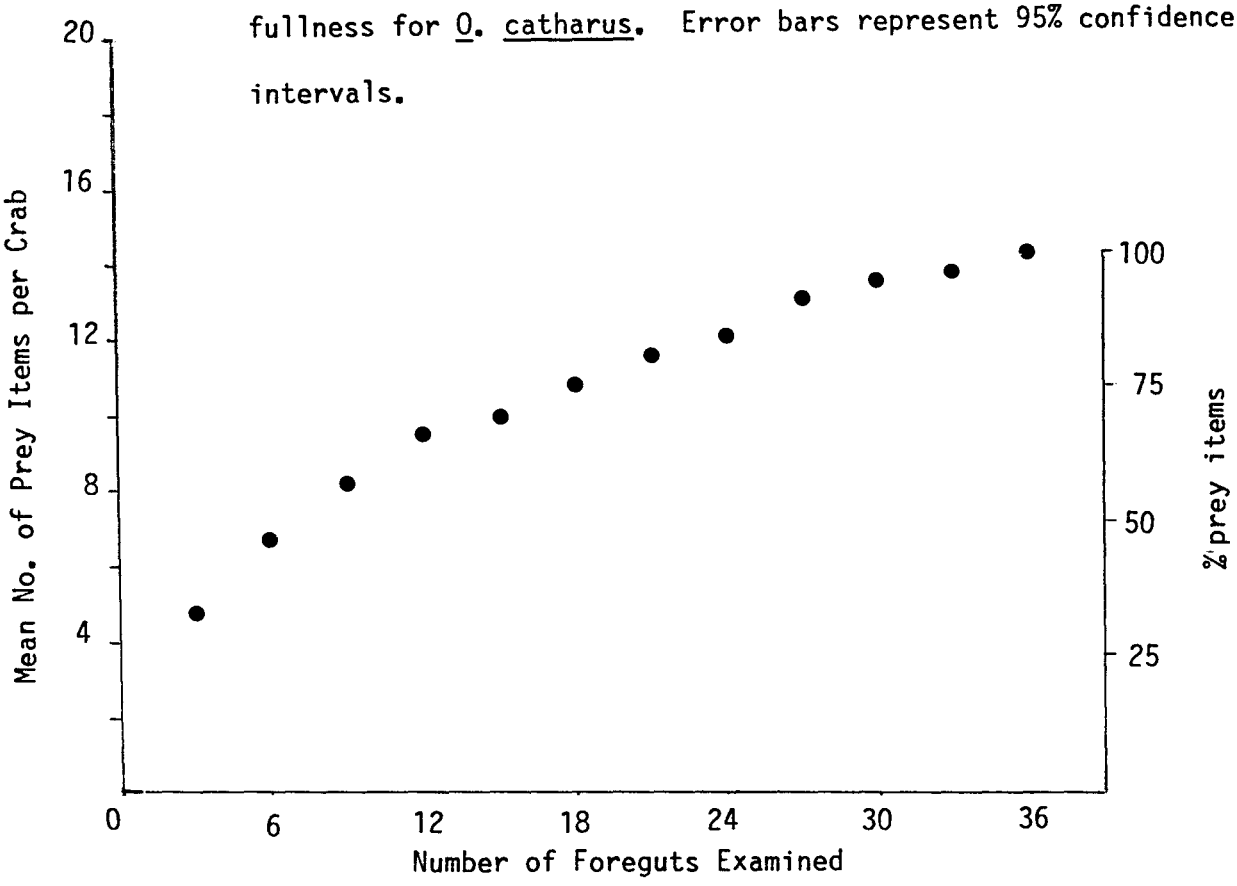

Fig. 34b. Mean number of prey items per foregut versus number of foreguts examined. Empty foreguts were not included in calculations.

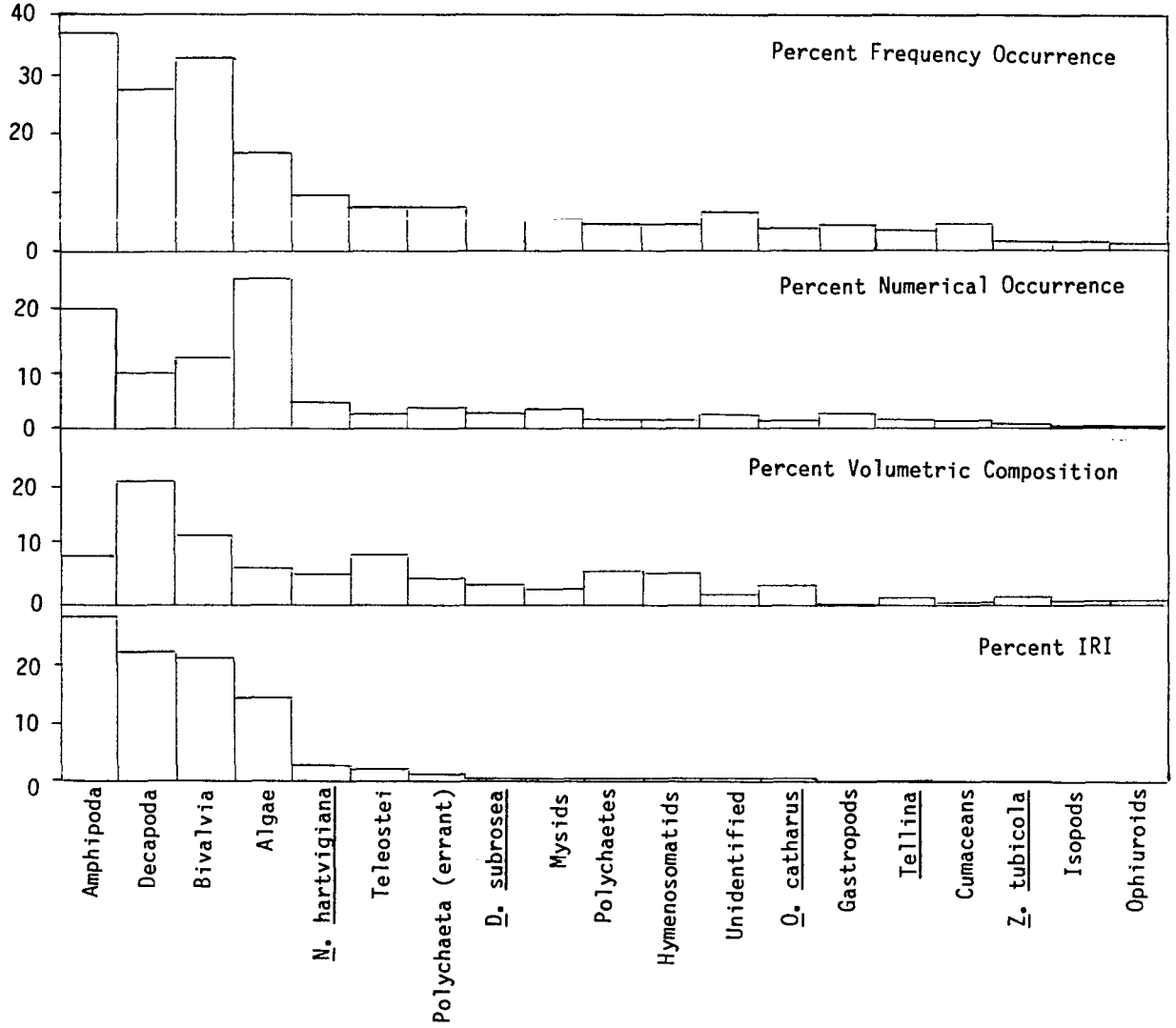

Fig. 35. Percentage composition of prey items found in the diet of O. catharus (<65 mm) calculated using: percent frequency, percent numerical composition, percent volume and percent Index of Relative Importance (IRI). Values represent combined years data from Little Alaloa.

sample sizes were small. A sample of no less than 12 crabs with more than 75% fullness would allow recognition of the major prey items in the diet of this crab. Measurement of the importance of rarer items in the diet would require larger sample sizes.

Diet Analysis Techniques

Dietary importance calculated for small crabs (<65 mm carapace width) using numerical, volumetric, frequency and IRI methods were compared using Spearmann Rank correlation coefficients (n = 178). Coefficient values between 0.72 and 0.97 ($P < 0.001$) suggested that these methods of assessing dietary importance for paddle crabs did not differ significantly. This is to be expected, as numerical, frequency and volumetric methods are components of the IRI equation. However, the importance of dietary items using numerical and volumetric methods varied considerably for particular prey items. Small prey items were under-estimated volumetrically while larger items were under-estimated numerically. Index of Relative Importance scores were most similar to frequency occurrence scores ($r_s = 0.968$, $P < 0.001$) (Fig. 35).

DISCUSSION

The Index of Relative Importance produces a dietary assessment comparable with the traditionally accepted frequency occurrence method. IRI has an added advantage, because its components are numerical, volumetric and frequency methods, of allowing each part of the equation to be investigated separately. In this way, prey items can be labelled according to their importance in crab

diet by numerical, volumetrical or occurrence methods. This study recommends dietary studies should not be based on volumetric or numerical methods alone as the reliabilty of these methods may be influenced by: crab feeding and masticatory structures, differential digestion rates (Hyslop, 1980) and type and size of food. Of the single methods of dietary assessment frequency occurrence gives the most accurate assessment. IRI yields more detail on the way prey items are important in the diet of crabs but requires the most work.

Differential digestion rates alter the quantity and types of food remaining in the foregut (Gannon, 1976; Hyslop, 1980; Williams, 1981). Frequency occurrence is therefore, biased in favour of prey items with hard parts which persist for long periods in the foregut, while prey composed of entirely soft digestable parts disappear rapidly (Williams, 1981). The degree to which these factors influence dietary accuracy may depend on the particular predator involved. The majority of prey items included in the diet of Ovalipes catharus have non-digestable parts which are easily recognised. Rapid clearance of food from the foregut and regurgitation of hard parts result in emphasis on recently eaten items. Predators consuming prey with no hard parts or having slow foregut clearance rates, and prey with hard parts, may require different approaches.

Accurate dietary studies should employ at least one method measuring number, and one measuring the bulk of food material present (Hyslop, 1980). IRI fulfills these requirements incorporating two measures of amount and one of volume.

Collection of no less than 12 foreguts each with greater

than 75% fullness is sufficient to pinpoint the most important prey items in crab diet However, the importance of rarer items or the changes in diet with season, time of day, temperature, sex, size, ovigerous state and diet selection behaviour may require larger sampling programs. The analysis technique used in a natural diet study is therefore, an important consideration.

APPENDIX 2

Data - Combined benthic replicates (nos/m^2)

Species	June	Sept	Dec	Mar
Amalda australis		24	8	8
Divaricella huttoniana				16
Dosinia sp.			8	8
Gari strangeri				8
Mactra ovata	16		8	8
Myadora striata			8	
Nucula hartivigiana				8
Panopea zelandica	1	1	1	1
Tellina (Macomona) liliana			21	
Tellina (Tellina) sp.			8	
Aglaophamus sp.	16	8		16
Armandia sp.				8
Cirriformia sp.	64	8		
Cossura sp.		36	8	
Glycera americana			8	
Heteromastides filformis	1328	256	72	9
Lepidastheniella sp.			8	
Lumbrinereis sp.			8	
Maldanidae sp.	16	72	8	80
Nereidae sp.		8		
Opheliidae sp.			8	
Ophelina sp.		8		
Orbinidae sp.	16			
Orbina papillosa	112	56	16	256
Paraonidae sp.	48	24		8
Pectinaria sp.		16		8
Polydora sp.		8		
Sabellidae sp.			24	16
Scolopos sp.	320	16	64	112
Sigalionicae sp.		16		
Sphaerodoridae sp.				16
Ostracod sp.#1	80	24	24	40
Leptostraca sp.				24
Diastylidae sp.	48	16		24
Tanaidae sp.				48
Amphipoda				
Anthuridae sp.	96		32	
Glycerida sp.				8
Janiridae sp.			8	
Helice crassa			16	
Pycnogonida sp.	16			
Ophiuriodea sp.	16			24

APPENDIX 3

Data - Combined drift algae replicates (nos/100g algae wet weight), collected from Little Akaloa, 1985-1986.

Species	June	Sept	Dec	March
Turbellaria sp.	2.8			
Nematoda sp.	18			
Amalda australis			1	
Patellidae sp.	2.8	0.4	0.8	
Pleurobrachiidae sp.			5.2	
Chitonidae sp.			0.8	
Sepioloidea pacifica				1
Cirratulidae sp.				1.2
Eunicidae sp.			2.8	
Lumbrinereis sp.	1.4			
Nereidae sp.	13.4		0.8	
Orbina papillosa				0.6
Perinereis sp.	2.8			
Ostracod sp.	1.4			
Mysid sp.	19.8	2.4	0.8	
Diastylidae sp.	2.8			
Allorchestes sp.	234	258	458	91.6
Atylus taupo	37.4	184	64	4
Amphipoda spp.	471	56	48.8	11.2
Caprellidae sp.	1.4			
Aegidae sp.	6.8	0.4		
Anthuridae sp.	1.4			1
Zenobiana tubicola	10.8	0.4	4.2	1
Cancer novaezelandiae			2.4	
Crangon sp.	11.8	7.4	8.2	12.2
Hemigrapsus crenulatus	1.4			
Halicarcinus cookii	0.8			
Halicarcinus innominatus			0.8	
Halicarcinus pubescens			16.6	
Hymenosoma depressum	10.8			1.6
Decapoda megalopa	2.8			
Ovalipes catharus	*	*	*	*
Petrolisthes elongatus	1.4	0.4		
Acarina sp.	1.8	0.4		
Achelia dohrni	6.8	8	22.4	4.8
Asternina regularus				4.8
Fellaster zelandiae	*	*	*	*
Rhombosolea retiaria				1
Pseudophycis bachus			5.2	
Total number of species	26	13	19	15
Total number per 100 g	865.6	517.8	643.4	135

APPENDIX 4

Data - Combined drift algae replicates (nos/100g algae wet weight) collected from Brighton Beach, 1985-1986.

Species	Oct	Dec	Mar
Hydroid sp.			*
Amalda australis			1.2
Perna canaliculus			362
Nereidae sp.			4.8
Perinereis sp.	7		
Sigalionidae sp.			1.6
Mysid sp.	395		2.6
Allorchestes sp.	1455	*	309.4
Atylus taupo	240	*	
Amphipoda spp.			22
Aegidae sp.			4.4
Zenobiana tubicola	103.5		50.8
Cancer novaezelandiae			2.4
Crangon sp.			1.2
Halicarcinus innominatus	21		18
Hymenosoma depressum	7		2.2
Decapoda megalopa			9
Ovalipes catharus	*	*	*
Petrolisthes elongatus	7		9
Peneidae sp.			3.8
Achelia dohrni	7		
Fellaster zelandiae	*	*	*
Ophiuriodea sp.			1.6
Pseudophycis bachus	*	*	*
Total number of species	12		21
Total number per 100 g	2242.5		806

APPENDIX 5

Data - Combined drift algae replicates (nos/100g algae wet weight) collected from Taylors Mistake 1985-1986.

Species	Oct	Dec	Mar
Hydroid sp.	*	*	*
Turbellaria	14		
Melagraphia aethiops			3.4
Perna canaliculus	14		*
Nereidae sp.			13
Perinereis sp.	14		
Mysid sp.	8		2.3
Allorchestes sp.	160	*	141
Atylus taupo	14		
Amphipoda spp.	8		35
Zenobiana tubicola	14	*	4.3
Crangon sp.	*		
Hymenosoma depressum	14		4.7
Decapoda megalopa	8		2.3
Ovalipes catharus	*	*	*
Petrolisthes elongatus			58.3
Peneidae sp.	2.3		
Fellaster zelandiae	*	*	*
Pseudophycis bachus	*	*	*
Total number of species	17		15
Total number per 100 g	284.3		266.6

* no values available